PLANT LIFE FORMS

By C. RAUNKIAER

Translated by

H. GILBERT-CARTER
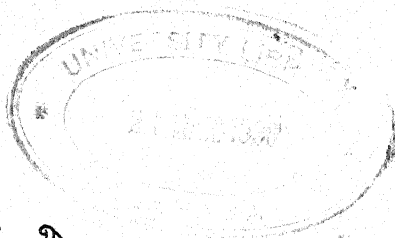
OXFORD
AT THE CLARENDON PRESS
1937

EDITORIAL PREFACE

THE separate publication in English of this little book, which was written by Professor Raunkiaer in Danish so long ago as 1907, is intended to introduce this part of his work to those teachers, students, and amateurs of botany to whom the much larger book (*The Life Forms of Plants and Statistical Plant Geography*, Clarendon Press, 1934) is not accessible.

Raunkiaer's great achievement is the description and classification, on a natural and easily intelligible system, of what are called the *life forms* of plants. We cannot be content with grouping the flowering plants, so far as their vegetative bodies are concerned, simply into trees, shrubs, and herbs. This does not tell us enough about their vegetative life: we must go farther.

Now the great majority of plants have to pass through a season of the year which is unfavourable to active life and growth—the dry season in hot countries, the winter in temperate countries. During this time the delicate growing points enclosed in the *buds* at the tips of the shoots are protected in various ways from being dried up and killed—sometimes by water-proof bud scales, as in the 'winter buds' of trees and shrubs, sometimes by being buried in the surface crust of the soil or quite deeply in the ground; or again by immersion in water or in the mud at the bottom of water. The degrees of protection thus afforded are very various and nicely adjusted to the requirements of the different species.

These are the characters which Raunkiaer uses to classify the life forms of plants; and he has shown very clearly that the species which live in a particular type of climate belong in large proportion to the kind of life form which is specially well adapted to that climate.

In this book he first explains the crucial features of different climates, and then describes the different life forms systematically and shows how they are adjusted to climates in which they live. The descriptions are fully illustrated by numerous examples, accompanied by very clear, accurate, and often beautiful drawings. The careful study of these descriptions and drawings, and comparison with living plants of the same and other species, will throw a new light on their structure and life economy for those who have never looked at plants from this point of view. It will serve as one of the best introductions to the study of our native plants in the field, because it calls attention to the ways in which they grow and maintain themselves. For these reasons it should be

to every one who loves plants.

Raunkiaer's book, though originally written thirty years ago, is not out of date, nor will it ever grow old, because it consists of careful, accurate description and simple natural classification of facts of nature which do not change.

A. G. TANSLEY

OXFORD
June 1937

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# THE LIFE-FORMS OF PLANTS AND THEIR BEARING ON GEOGRAPHY

PREFACE

In this little book I have attempted to classify and describe the life-forms of plants as a basis of biological Plant Geography by using in my definitions of the life-forms only those structural characters that reflect the essential dependence of the plants upon climate, i.e. their adaptation to survive the unfavourable season. Here then Plant Geography as botanical science gives place to Plant Geography as geographical science. We shall consider vegetation as an expression of the climate, and the life-forms of plants as a means of determining the biological characteristics of the different climates.

As long ago as 1903 I made a statement of this general theme and later elaborated it in *Videnskabernes Selskabs Oversigt* for 1905. This account is written in French and is not easily accessible, and as I consider that others besides professional botanists might perhaps be interested in my views, I have here attempted to give a more popular account of them written in Danish and illustrated with figures, some of which are from my book *De danske Blomsterplanters Naturhistorie*, Vol. I, and some of which are new. Most of the illustrations have been drawn by my wife, Mrs. Ingeborg Raunkiaer.

The information about the structure of the individual plants is in part already known, especially from the works of Irmisch and Warming, and in part is the result of my own investigations; but I did not think it necessary to overburden the descriptions by mentioning which facts are new and which were already known, especially since the morphological and the physiological relationship have one and only one significance in illustrating my principal theme, which is a coherent sketch of life-forms accurately defined and the relationship they bear to the climate.

My thanks are due to the Committee of the Carlsberg fund. It is their assistance that has made it possible for this work, in spite of the probability of a small circle of readers, to appear as a book.

<div align="right">C. R.</div>
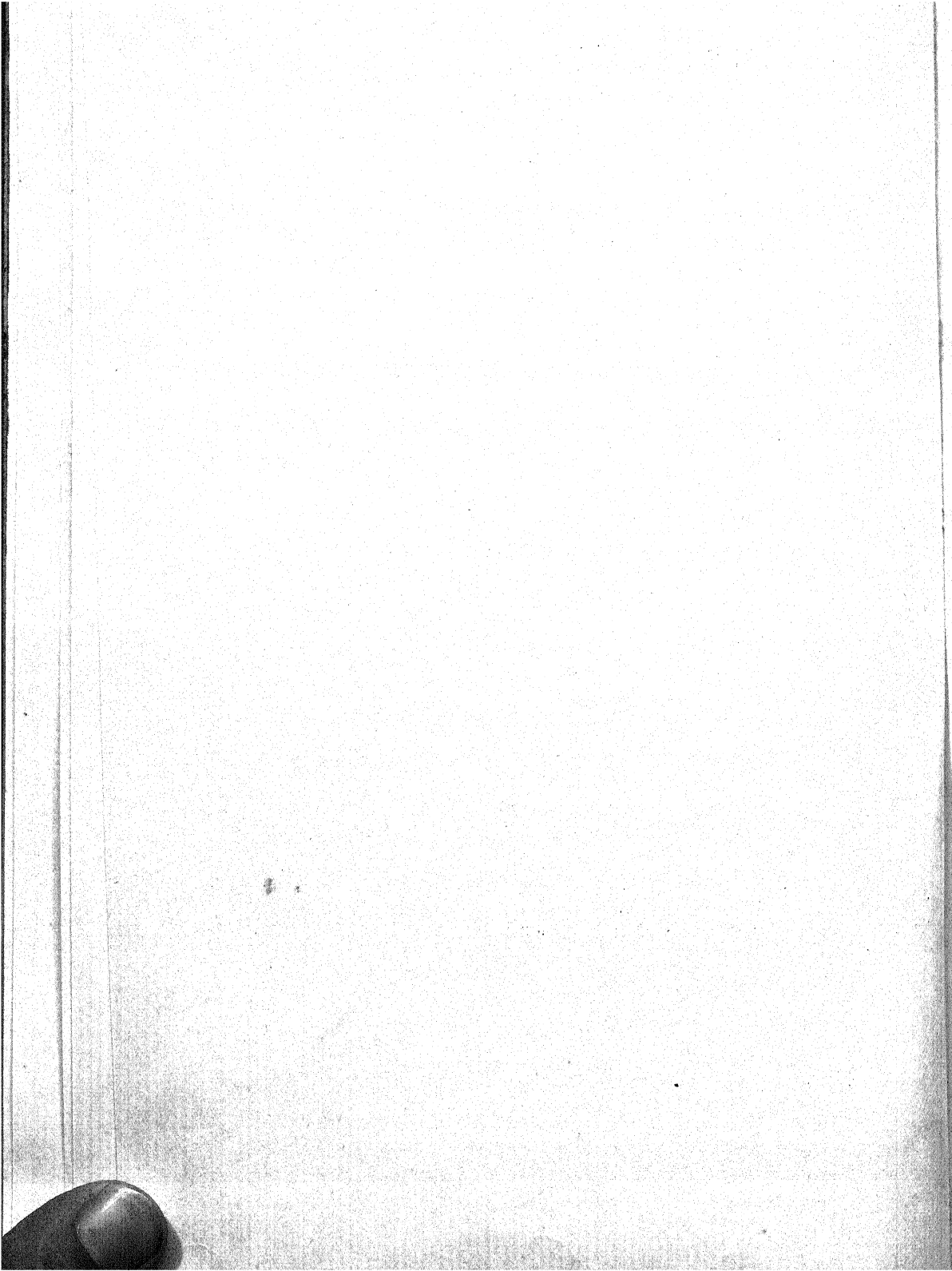
INTRODUCTION

THOUGH we know neither what life is, nor whence the first germs of life arose, yet there is no reasonable doubt that all the myriads of diversely fashioned plants and animals inhabiting the world to-day are the result of the process of evolution.

In the absence of certain knowledge opinions are divided about the mechanism which brings new species into being.

Some investigators think that new species arise congenitally, that is to say, that individuals arise which differ from their parents in potentialities and properties, and that some of these differences, which are demonstrably hereditary, are handed on to their offspring, making the primordia of a new species. This, known as the Darwinian Theory, has recently been amplified and placed upon an experimental basis chiefly by the Dutch botanist Hugo de Vries, who calls the forms which show hereditary deviations mutations. His theory is called the mutation theory. It can scarcely be doubted that new species can arise in this way; but the causes of the mutations are unknown.

Others think that it is the environment that makes new species; that individuals arise having identical structure and propensities, and that these individuals growing and developing in different environments come to differ from each other in form and structure. As a matter of fact these differences are almost certainly not hereditary in the ordinary sense of the word, and do not occur again in the offspring which grow in an environment differing from the one that brought about their existence, so that they cannot be looked upon as the beginnings of new species. But even if the difference brought about by the environment, i.e. the acquired characters, is not directly transmissible, yet the possibility is by no means excluded that a gradual alteration takes place in the individuals, so that in the course of many generations of growth in a different environment they gradually come to inherit the peculiarities impressed on the individuals by this environment when the environment which caused these peculiarities is no longer present. Thus one can imagine a species gradually becoming split into several species by growth of individuals during long periods in environments differing widely from the original one. There is much in nature which makes it difficult for us to doubt that this is one of the sources of new species; but exact scientific proof can only be obtained by means of cultural experiments carried out during decades or even centuries, and such experiments can scarcely be carried out by an individual investigator, but need Phylogenetic Institutions guaranteed by the State. As yet no such institutions exist.

Others believe that new species arise by hybridization, and we can

scarcely doubt that this may take place. These three possible modes of origin of new species are not mutually exclusive, but presumably can operate at the same time. Exact experiments to illustrate this problem are only in their infancy.

But in whatever way species arise it is certainly the environment that determines the destiny of the species, determines whether they shall perish as unfit for life or whether they survive to be a link in the chain of species. It is the environment that determines the place in nature occupied by the individual species. Often more individuals are produced than there is room for. Competition for space and food of necessity entails that each individual species shall within limits become confined to those situations to which it is best adapted and better adapted than the other competing species. In all places where the plant community is dense and there is competition for space and food we may safely assume that there is complete harmony between the species and their environment, in other words that the plants are adapted to their environment. It was Darwin who first opened our eyes to the fact that this adaptation, this orderly arrangement of the world, was not an incomprehensible phenomenon, but the necessary consequence of the relationship between the environment and the demands of the individual organisms. The structure of any plant is not in itself effective; it is the relationship to its environment that will show whether an organism is constructed on a plan favourable to its life. A plant of *Corynephorus canescens* with its marked xerophily is not serviceably constructed in relation to itself; this plant would perish if there existed none of the peculiar dry localities on which it is able to live and win the battle with competing species. It is the environment, the competition, &c., which determine the place of the species in nature; adaptation follows as a derived phenomenon. The environment determines everything.

Most plants produce many seeds which are distributed with more or less facility, bringing the individuals gradually into places where they are best adapted to live. But since the methods of migration and the factors which limit it are manifold, and since many species migrate slowly, it often happens that plants have not yet arrived at places where under the present conditions they are best adapted to live, and have not yet arrived at all places where they are better adapted to live than the species which at present occupy those places. We see this by the behaviour of certain species introduced by man into new territories; in some localities such aliens have succeeded in partially supplanting the original vegetation. But in most parts of the world where cultivation has not interfered excessively with nature the plant world is doubtless in a kind of equilibrium, the individual species growing in environments to which they are best suited. But this equilibrium is not constant, for the environment is always altering, slowly, it may be, in some places, and faster in others.

Since the time of Darwin the study of the correspondence between the demands of plants and the environments in which the plants grow has influenced botanical science deeply. This subject is boundless; the number of species amounts to hundreds of thousands, and the demands of each species are manifold. Plants are dependent for pollination on insects and on the wind, for seed distribution they are dependent upon animals, wind, water, &c. But this is not the subject that concerns us; we are interested in the plant's dependence upon factors which bring about its vegetative welfare and in the resulting dispersion of the species on the earth's surface; in other words in how the demands of plants are expressed in various life-forms in harmony with the various environments offered by the different regions of the earth.

All over the world environments varying from place to place determine the existence of different life-forms, because the demands of the plants, which are, at any rate partially, expressed by their structure, must of necessity be in harmony with the environment, if life is to continue. The plant world therefore varies from place to place. In order to obtain a clear view of the complexity involved we must find out what in the main is common to equiconditional regions and to the vegetation of these regions. Since it is much easier to determine the environment than the demands of the plant, the best results are to be expected by beginning with the environments and trying to define those which are in the main alike. In investigating the plants within these individual environments we must first try to discover the chief peculiarities in their structure, the life-forms by means of which the harmony between the plant world and the environment has expressed itself clearly. The requirements for the life of plants are all of equal importance inasmuch as none of them can be dispensed with; but when these requirements are used as a foundation for dividing up the earth into equiconditional regions they are very far from being of equal importance. Some, for example the amount of oxygen and carbon dioxide in the air, differ so little in different places that they have no significance for the life-forms, and therefore cannot be used as characters for equiconditional regions. Others, for example the chemical and physical nature of the soil, the relationship between plants and animals, and between plants themselves, vary so widely even within the smallest districts that they cannot be used for limiting large equiconditional regions; but on the other hand they are useful in the detailed analysis of vegetation within these regions.

The same is approximately true of light. If the demand for light always expressed itself sufficiently obviously in the structure of plants, and if the plants were all of equal height and shaded each other equally, then the different intensity of sunlight in the different degrees of latitude would be an important factor for limiting large equiconditional areas.

But there is a vast difference in the size of plants, and some grow in the shade of others, so that the relationship of light even in very small areas differs so greatly that it is impossible to use it for determining what is common to the environment over extensive tracts.

The most important factors determining the environment which still have to be mentioned are moisture, water (here more closely defined as precipitation), and temperature. Temperature regulates transpiration and thus alters the significance of the amount of water present. The relationship of temperature to humidity is the factor which makes the deepest impression on vegetation at the present epoch. Heat *quâ* heat certainly plays a very important role in the distribution of plants. Each species demands its own degree of heat, and consequently each occupies a corresponding geographical position. Megatherms[1] demand much heat, and will only grow where the temperature is relatively high throughout the year; they are consequently found only in the tropics. Mesotherms can endure a considerably lower temperature during a longer or shorter period of the year; they can grow in tropical and sub-tropical regions; but it is only in the sub-tropical region that they can conquer competitors which demand a different degree of heat. Microtherms are plants of the temperate regions. They demand a still lower temperature, not needing so high a summer temperature, and enduring a much lower winter temperature. It does not necessarily follow, however, that the plants mentioned grow best under the physical and chemical conditions available. All that is meant is that under these conditions they are able to prevail against competitors which demand a different degree of heat. A fourth group, Hecistotherms, comprises plants belonging to the cold regions. They have the lowest heat demand of all plants, will grow where the summer is short, and are able to endure a long and very cold winter. In spite of the fact that heat *quâ* heat has such great importance in determining the distribution of plants, yet it is impossible to use heat as the basis for delimiting equiconditional regions and characterizing these regions by their plant life. The reason of this is that the temperature demanded by plants has scarcely any influence on their structure, or perhaps it would be better to say that our knowledge is at present insufficient to enable us to draw from a plant's structure any conclusions about its heat demand. If our knowledge were sufficient to enable us with ease and certainty to determine the heat demand of a plant from its structure, then temperature would become perhaps the most important factor in delimiting equiconditional regions. But at present the use of temperature for this purpose must be imperfect, as we have to rely on our knowledge of the temperature in which

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[1] This and the following terms are here used to signify only the different demands for heat by plants. A. de Candolle, who first used them, included, at any rate partially, demands for moisture as well.

plants grow in a state of nature. On the other hand temperature as a factor affecting transpiration is recognized as a very important character in delimiting equiconditional regions.

Though the factors necessary for plant life are, as I have said before, of equal importance, inasmuch as plant life cannot exist in the absence of any one of them; yet it is not incorrect to say that some factors are more important than others. The same kind of relationship prevails between the plant and the ten elements which are necessary for its perfect development. All these elements are equally important in that each is necessary for the development of the plant; but the element which is present in the smallest quantities plays the most important part because it *is* present in such very small quantities; its complete absence would prevent the development of the plant altogether. This element then might be considered more important than the others. The same is true of environmental factors in general: the necessary factors which are present in the lowest degree are comparatively of most importance, because their complete absence can stop the further distribution of plants, and thus become factors defining regions of common environment.

Of all the factors necessary for plant life water is the one which over vast expanses of the earth's surface most nearly approaches the status of a limiting factor. This is true even of regions where a sufficiency of water is actually present, as it is in extensive tracts in the colder regions of the world, where at some times of the year the temperature is so low that the plants cannot absorb the water; they can actually die of drought standing in saturated soil, perishing of what Schimper calls physiological drought, which has the same effect on plants that physical drought has in warmer and drier regions.

While then, in addition to the fact that the water demand of plants compared with their other demands usually finds marked expression in their external and internal structure, the relationship of plants to water influences vegetation to such a degree that it is by far the most important factor in the 'plant climate'—we can, in fact, use the structural expression of the demands of plants as a reagent, as it were, to 'test' their environment. The series of types we are thus able to make will at the same time reveal the historical development of the plant world, of the changes that have taken place throughout the ages according to the operation of fixed laws. This we can do because there is every reason to suppose that such water conditions in the course of time have become increasingly unfavourable to plants, and that species have gradually arisen which are essentially new in that their demand for water has decreased in harmony with the curtailment of available water. The series of types then is a natural one; it is the expression of an organic development.

We may safely assume that the conditions of life were formerly more

favourable than they are now. There was a time when heat and moisture were less dependent upon seasons than they are now. The luxuriance of vegetation during the Carboniferous age and the uniformity of that vegetation in all parts of the world lead us to suppose that the climate must have been warm and humid and approximately constant from the Equator to the Poles.

But gradually, as dissimilar areas became differentiated, the character of the vegetation became differentiated too. This was because the deterioration of the environment in any region destroyed those species whose demands were too exacting, and of the new species which arose only those could survive whose demands could be satisfied by the environment. Thus existing vegetation is not only an expression of conditions to-day, but it also is a link in the chain of organic evolution, a chain which has been forged by alterations of the environment.

We must then consider the life-forms belonging to constantly warm and constantly humid regions as the most primitive life-forms, and the life-forms adapted to other climates as later developments. There is, for example, no doubt that trees and shrubs with covered buds arose later than those with naked buds; that species adapted to life in an unfavourable climate by bearing their buds on underground shoots have arisen later than those life-forms which do not possess this peculiarity. There is then good reason to characterize life-forms simply by the means through which they are able to exist in progressively more unfavourable environments which have arisen because of the gradual changes in climate.

But this statement needs qualification. The important point is that environments not only differ in space but in time. Conditions differ not only from place to place, but in the same place from month to month. The seasons impose different conditions. Apart from the tropics, where the climate is always warm and humid and thus fairly uniform and favourable during the whole year, all other regions have at least two seasons, a favourable and an unfavourable, or more correctly a more favourable and less favourable season. Those structural characters which enable plants to harmonize the demands of their vegetative organs with their environment are on the whole the characters which make the most obvious impression on vegetation. From the nature of the case, however, the difference between the favourable seasons of two regions must be far less than the difference between their unfavourable seasons. This makes it exceedingly probable that those structural differences which enable plants to survive unfavourable seasons are greater than those which harmonize the same plants with the favourable seasons. If we then wish to use vegetation as a test of the plant climate, to delimit the equiconditional regions by means of the vegetation of those regions, we must, I think, do so by observing the structural peculiarities which enable the plants to survive the unfavourable seasons.

Since water in relation to temperature has the greatest significance in defining equiconditional areas, and since those two factors rise and fall during the course of the year, it becomes of great interest to make clear diagrammatic illustrations, such as are shown in Figs. 1–6, of the relationship of these factors in given regions during the course of the year.
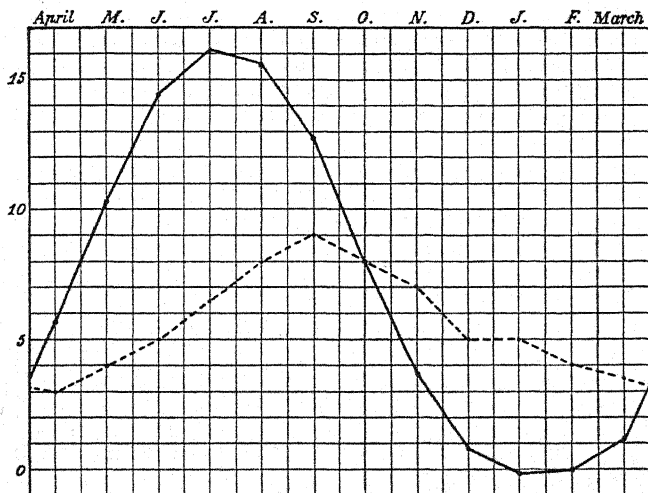

FIG. 1. Hydrotherm figure for Denmark. —— Temperature curve; - - - - - - Precipitation curve. The numbers denote degrees Centigrade for the Temperature curve and centimetres for the Precipitation curve.

The figures on the vertical line to the left denote degrees Centigrade; the names of the months are given on the horizontal line above, beginning with April for the Northern Hemisphere and with October for the Southern Hemisphere. On the vertical lines the mean temperatures of the months are given, and the points marked with these mean temperatures are joined by a ruled line: the temperature curve thus resulting portrays the yearly variations of temperature in the locality in question. The precipitation curves are made in the same way. As far as I know these two curves have hitherto always been made separately, but here we can look at both together; indeed, both curves are combined in the same figure, the same number on the vertical line to the left representing degrees Centigrade for the temperature curve and centimetres for the precipitation curve. In the figures the ruled line always represents the temperature curve and the dotted line the precipitation curve.

The favourable and unfavourable seasons, in so far as they are dependent upon the two essential factors, heat and moisture, are shown in these figures as crests and troughs in one or both curves. The two troughs may occur at the same time of the year or at different times.

Thus each equiconditional region shows a characteristic figure which I shall here designate its hydrotherm figure, and which exhibits the most important environmental properties of the district.

The most important adaptation for plants is that which enables them to survive the seasonal trough. I have therefore used as a basis for defining life-forms, that are to characterize equiconditional regions, structural peculiarities which enable the plants to survive the unfavourable seasons. Now all parts of plants are not equally sensitive to the effects of the unfavourable seasons. The young embryonic tissue of the growing points is the most sensitive of all, and since it is this very tissue on which the plant's continued growth depends, it is of the greatest possible importance that it should survive the unfavourable season unscathed. I have therefore delimited the life-forms by means of the kind of protection which enables the growing points to survive the unfavourable season.

Before giving a detailed description of the life-forms I will give a short account of the most important hydrotherm figures for the equiconditional regions to which the life-forms correspond.

In order that conditions may be favourable there must be a certain relationship between the temperature curve and the precipitation curve, there must be a definite hydrotherm figure. If the temperature curve is high the precipitation curve must be high too if the conditions are to be favourable. A high temperature promotes transpiration, so that precipitation must be abundant in order to make good the water thus lost.

In tropical regions, apart of course from mountainous districts, the temperature curve remains high all the year round; the temperature is thus sufficiently favourable for the continuous vital activities of plants. It is the course of the precipitation curve which here demarcates the great regions. There are of course imperceptible gradations between the different types of precipitation curve, from high precipitation all the year round (Fig. 2), through different degrees of varyingly high precipitation (Figs. 3 and 4) to very low precipitation all the year round (Tropical desert regions). We must not suppose therefore that large and extensive regions have approximately the same environments. The expression 'equiconditional regions' must not be taken literally; it is only meant to imply that in certain broad features there is approximate uniformity in the vegetation, which shows in those regions the same relationship to the life-forms composing it. In spite of the imperceptible gradations encountered we are obliged, in order to obtain a clear view of the matter, to draw boundaries. It is important that these boundaries should be as natural as possible.

In certain comparatively well-demarcated tropical regions, e.g. parts of the East Indies, especially the East Indian Islands, the West coast of

Africa, parts of South America, especially the region of the Amazon, &c., the climate is not merely constantly warm, but it is also constantly wet; the precipitation is high throughout the year. This is seen in the hydrotherm figure for Sumatra (Fig. 2). The conditions are favourable throughout the year, and there is no really unfavourable season; the vegetation is composed of the least protected life-forms; even the most exacting demands for water and heat can be satisfied. From this ideal state of affairs there are two divergent lines of climates. Firstly, we have the
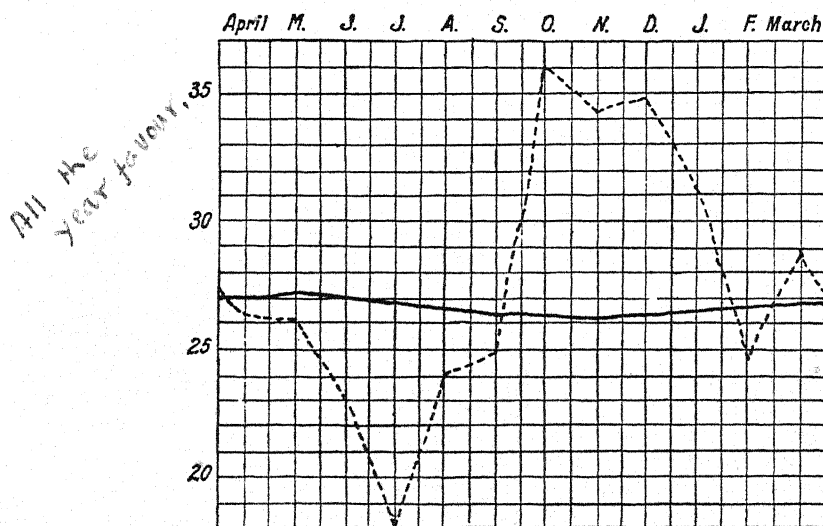

FIG. 2. Hydrotherm figure for the East coast of Sumatra near the Equator.
Numbers, &c., as in Fig. 1.

tropical series with the constantly high temperature curve, but with the decreasingly favourable precipitation curve. Secondly, there is the series of climates outside the tropical regions extending through the subtropical zones of the temperate and cold parts of the world. These climates have a different kind of temperature curve, and their precipitation curves differ widely.

Within the tropical series of climates we can differentiate, apart from the constantly humid regions, at least two main areas. In the first of these the precipitation is still comparatively high, but its curve shows a very marked trough, signifying that the precipitation is unevenly distributed during the course of the year. These regions have two different seasons, a rainy season and a dry season. The boundary line between this and the foregoing region must be drawn in accordance with statistical investigations of the comparative relationship between the life-forms. Owing to the high temperature, if the precipitation amounts for a long period to less than 5 cm. a month a great change is seen in the

relationship of the life-forms. But it is apparent that if the yearly precipitation is fairly high, the vegetation can well tolerate a falling of the precipitation curve for a single month to below 5 cm. without causing essential change in the composition of the flora as far as life-forms are concerned (Fig. 3).
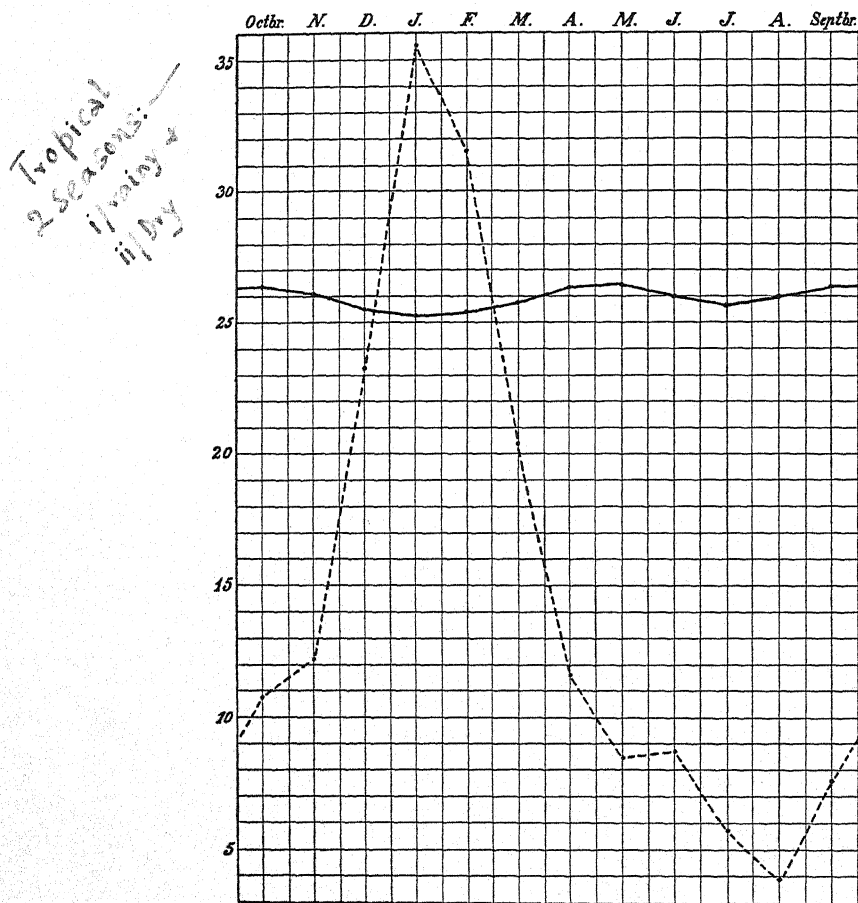

FIG. 3. Hydrotherm figure for Batavia. Numbers, &c., as in Fig. 1.

We can here scarcely speak of an actually dry season if the precipitation curve during two months or more does not fall below 5 cm. In that equiconditional region known as the savannah region, where there is a marked dry season in combination with a yearly precipitation which is not excessively low (Fig. 4), the dominant life-forms differ from those of the regions of tropical rain forests. It is probable that statistical investigation of life-forms will make it necessary for us to divide the savannah region into two or more regions.

Where the precipitation curve as a whole sinks very low because the annual precipitation is very small, we find tropical deserts, and with
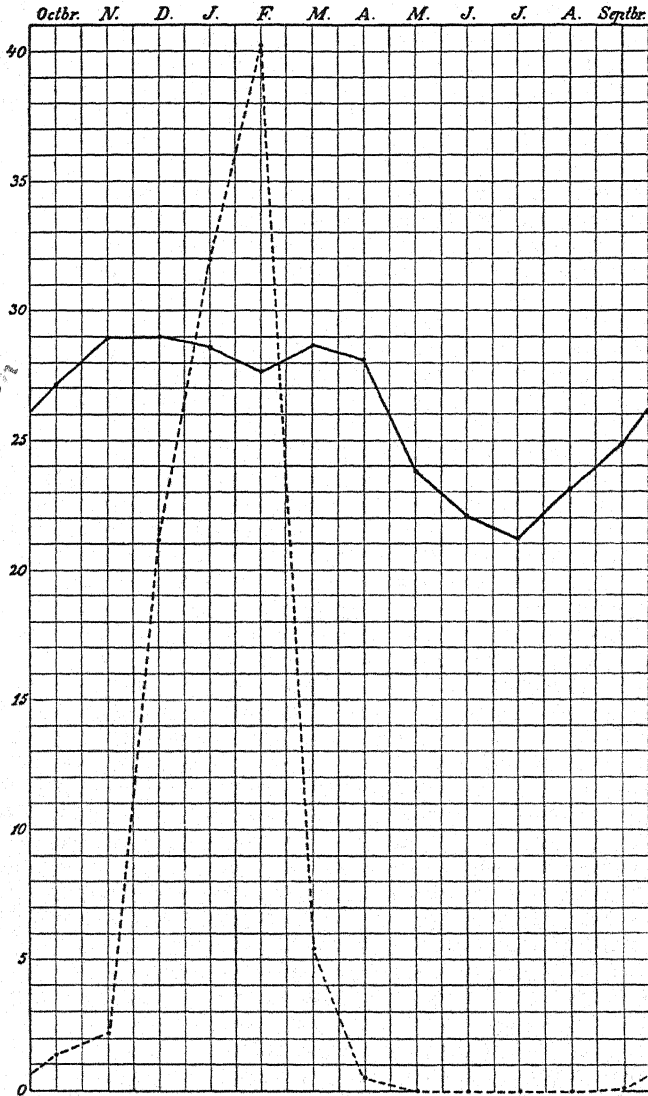

FIG. 4. Hydrotherm figure for Sweers Island, at the head of the Gulf of Carpentaria. Numbers, &c., as in Fig. 1.

these perhaps we might unite the sub-tropical deserts, calling them respectively, Megathermic and Mesothermic deserts.

In the sub-tropical zone the temperature and the precipitation curves both show a conspicuous trough. Apart from the tropical deserts and

steppes, where precipitation is low, the sub-tropical zone is divided into two equiconditional regions, the region of sub-tropical winter rain and the region of sub-tropical summer rain. In the first of these regions the trough of the precipitation curve occurs at a different season from that of the temperature curve (Fig. 5), so that we get a dry summer and a more or less humid winter. In those parts of the sub-tropical regions with summer rain the troughs of the precipitation and temperature curves
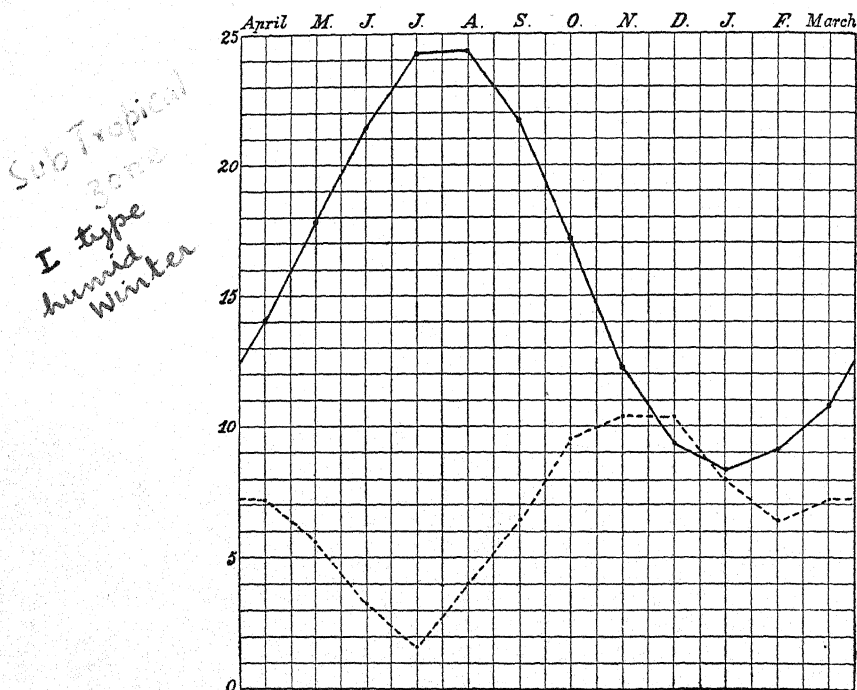

FIG. 5. Hydrotherm figure for South Italy. (Temperature curve is that of Naples.) Numbers, &c., as in Fig. 1.

occur at the same season (Fig. 6), so that we get a wet summer and a comparatively dry winter. This difference in the climate of the two regions is clearly expressed by the relationship of the life-forms composing their vegetation.

Where the dry season is especially long and the precipitation low sub-tropical steppes occur, and these pass imperceptibly into the corresponding steppes of the temperate zones or into sub-tropical deserts.

While in the tropical and for the most part in the sub-tropical regions it is the course of the precipitation curve that demarcates the regions characterized by different life-forms, in the temperate and especially in the cold regions on the other hand it is the temperature curve which is decisive; the precipitation curve in these regions being high in relation-

ship to the temperature curve (Fig. 1). In certain districts however the precipitation causes a covering of snow in winter, and this is of great importance in delimiting regions dominated by the same environment. I shall not here enter into the problem of delimiting equiconditional areas in the colder parts of the world, where the different regions pro-
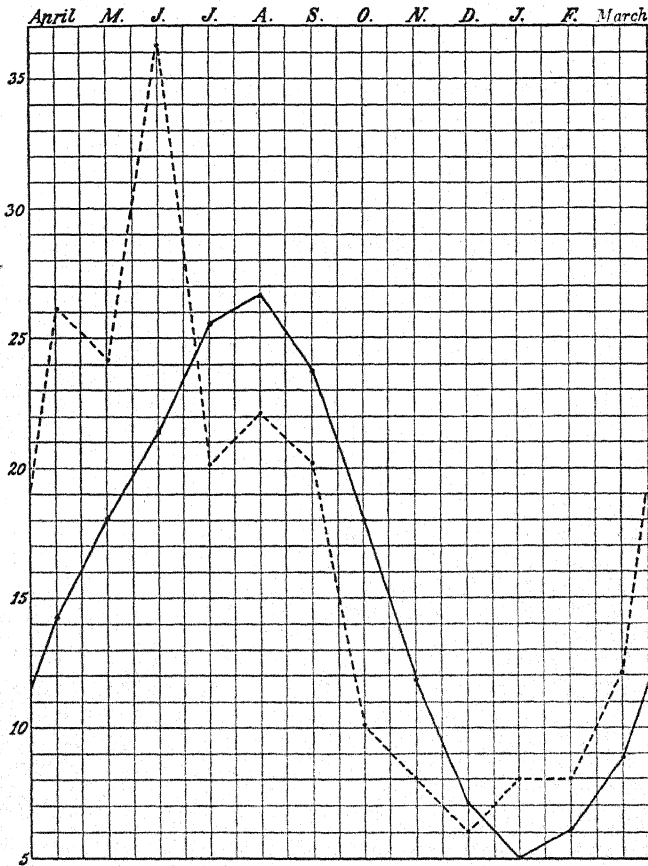

FIG. 6. Hydrotherm figure for South Japan (Nagasaki). Numbers, &c., as in Fig. 1.

bably show a wide difference in their hydrotherm figures, without, however, causing such a marked difference in life-forms as is seen in the tropical regions. The reason for this peculiarity is that the life-form specially adapted to colder regions, viz. the Hemicryptophyte, is only above the ground during the favourable season; in the unfavourable season it is protected by the soil, and therefore less influenced by the degree of severity of the unfavourable season.

Now that we have completed our short description of the great

equiconditional regions let us study the life-forms which belong to them, and in order to understand the matter fundamentally let us first describe the five main types of life-form.

LIFE-FORMS (BIOLOGICAL TYPES)

In order to arrange life-forms in a natural series corresponding with their evolution, we must first ask the questions: 'which life-form must be looked upon as the most primitive, which can be regarded as standing in the relationship of parent to the others?'

If we take for granted that the most primitive life-form is the one that is best adapted to life in the most primitive climate, our question may then be altered to, 'which of the climates now existing is most like the climate that may be supposed to have prevailed on the earth when flowering plants arose?' It is generally supposed, and with good reason, that the climate in former periods of the earth's history was more uniformly hot and moist than it is now. Granted then that the constantly hot and constantly moist climate, which now prevails in certain tropical regions, is more primitive than the other climates of to-day, we can regard as most primitive the life-form best adapted to such a climate. From such a life-form all others must be derived, and must be regarded as adaptations to climates which have arisen later.

In a constantly hot and moist climate plants can go on developing new shoots; there is nothing in the environment that hinders the continual growth of the individual. In such a climate we therefore find chiefly plants whose shoots project into the air, continuing their life from year to year after the manner of trees and shrubs. I use the word Phane-rophyte (Fig. 7, 1) to designate plants whose stems, bearing the buds which are to form new shoots, project freely into the air. If we examine Phanerophytes more closely we may divide them into sub-types according to whether their buds are more, or less, protected. We may differentiate, for example, evergreen Phanerophytes without bud-covering, evergreen Phanerophytes with bud-covering, and deciduous Phanerophytes with bud-covering. The size of plants has a very definite bearing on their relationship to humidity, so that we may further divide the Phane-rophytes into Mega-phanerophytes, Meso-phanerophytes, Micro-phanerophytes, and Nano-phanerophytes.

Phanerophytes, especially the least protected among them, are the plants of those portions of the earth which are most favoured climatically. In tropical regions which are constantly warm and constantly moist, they form the bulk of the species; but as we leave the tropics and reach less and less favourable climates, climates with a long and hot dry season, or climates with a severe winter, we find that Phanerophytes decrease in proportion to the remaining life-forms. In these less favoured localities

we meet only the best protected sub-types of Phanerophytes, especially those which in the unfavourable season lose their leaves and whose apical shoots are protected by bud-scales. Gradually, as we approach the boundary beyond which Phanerophytes cannot live, they become lower and lower in stature till we meet only small bushes and dwarf trees. Because of the lowness of their growth these plants are not as exposed to the dangers of excessive transpiration as the tall Phanerophytes. Indeed, in regions where snow lies in the winter they are often so low as to be protected by the covering of snow; thus forming a transition to the second main type of life-form namely the Chamaephyte. Finally in the far north, in the higher regions of lofty mountains, and in dry steppes, the Phanerophytes disappear altogether.

The Chamaephyte, the second main type, is characterized by having the surviving buds situated close to the ground. This position may come about either because the whole shoot lies flat on the ground (Fig. 7, 3), or because the distal portion of the shoot, which projects into the air, dies at the beginning of the unfavourable season, so that only the shoot's lowest portion together with the surviving buds remains behind (Fig. 7, 2). In Cushion plants the surviving shoots are densely massed together and so short that the plants may be considered to be Chamae-phytes.

The third type is the Hemicryptophyte which has the surviving buds actually in the soil-surface, protected by the soil itself and by the dry dead portions of the plant (Fig. 7, 4). The aerial shoots, bearing leaves and flowers, survive for only a single period of vegetation, and then die back as far as the part of the shoot situated in the ground and bearing the surviving buds. The majority of our biennial and perennial herbs, and indeed the bulk of plants in the cold and temperate parts of the earth, belong to this life-form, which can be subdivided according to whether the shoots are more or less modified for their life in the soil.

The Cryptophyte, as the fourth type is called (Fig. 7, 5–9), is characterized by having its buds completely concealed in the ground or at the bottom of the water. The depth at which the buds are buried varies in different species. This life-form is better protected against desiccation than the Hemicryptophyte, and it is specially adapted to regions with a longer dry period; hence steppes are especially rich in Cryptophytes. Many herbs with horizontal root-stocks (Fig. 7, 5) and the majority of bulbous and tuberous plants belong to this life-form (Fig. 7, 6). In the favourable season they send up shoots bearing leaves and flowers: in the dry period the plant is lost to sight, the buds being hidden at a greater or less depth in the ground.

The four life-forms mentioned show a series of progressions in the same direction. As we travel away from the most favoured portions of the earth, which are characterized by Phanerophytes, to less clement
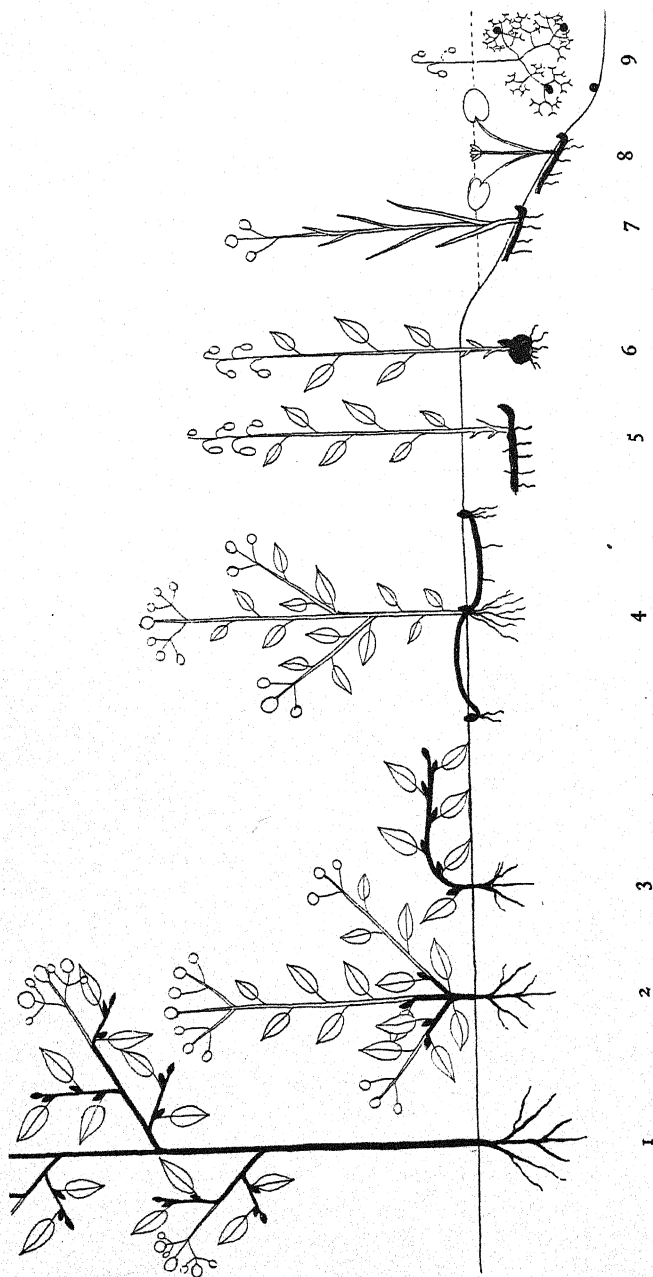
FIG. 7. Diagram of the first four types of life-form: Phanerophytes (1), Chamaephytes (2–3), Hemicryptophytes (4), and Cryptophytes (5–9). The parts of the plant which die in the unfavourable season are unshaded; the persistent axes with the surviving buds are black. Proceeding from Phanerophytes on the left and going farther and farther to the right, it is seen how the plants enjoy progressively better protection during the unfavourable season, the surviving buds being attached lower and lower. In Chamaephytes the buds are on the surface of the ground (2 and 3), in Hemicryptophytes they are in the soil-surface (4), and lastly in genuine Cryptophytes (5 and 6) the buds are actually in the soil, or at the bottom of the water in Helophytes (7), and Hydrophytes (8–9).

climates, we observe a tendency for surviving buds to be borne, firstly near the surface of the earth (Chamaephytes), secondly in the soil-surface (Hemicryptophytes), and finally entirely buried beneath the soil or water (Cryptophytes), where of course they are best protected from desiccation, which is their greatest danger.

The fifth life-form, the Therophyte, comprises plants which complete their life-cycle within a single favourable season, and remain dormant in the form of seed throughout the unfavourable periods. The shorter the time that these plants take to complete their life-cycle, the more unfavourable the climate they are able to endure. Because these plants are able to complete their life-cycle in a comparatively short period, often in a space of a few weeks, this life-form is the best protected of all. Therophytes disappear entirely during the unfavourable season of the year, existing only in the best protected state of all, that of the seed. They abound particularly in unfavoured portions of the earth, such as steppes and deserts.

I. Phanerophytes

By Phanerophytes I mean plants whose buds and apical shoots destined to survive the unfavourable period of the year project into the air on stems which live for several, often for many, years. In Phanerophytes the primary shoots, and often also certain lateral shoots, are negatively geotropic, so that the buds are bound to be carried upwards. The direction assumed by branches has been shown to be due to several causes. It may differ not only in different species, but in different individuals of the same species, and even, indeed, in different branches of the same individual. These diversities are largely responsible for the peculiar habit of individual plants.

Apart from certain weeping trees, which I shall discuss later, the shoots of all Phanerophytes are more or less negatively geotropic, but the direction of their growth is usually determined by other causes than geotropism, so that the angle they subtend to the mother axis and the direction they take up in space are exceedingly various. In fastigiate trees the shoots grow erect, forming an acute angle with the stem (e.g. *Populus italica*). There are innumerable gradations between fastigiate trees and those whose primary branches arise at an angle of 90°, an arrangement common in the *Coniferae*. The antithesis of the fastigiate trees is the weeping tree, whose branches, or at least some of them, hang downwards, especially towards their apices. In so-called 'passively weeping trees' it is the weight of the branches that causes them to arch towards the ground. In these trees most of the young shoots, as long as they are so short that their rigidity can maintain them in a definite position, ascend more or less obliquely according to the angle they subtend to the mother axis. Gradually as the branch lengthens without

its rigidity increasing sufficiently to maintain it in an erect position, it sinks more and more, finally becoming pendulous. The apex is often horizontal, or it may ascend to form an S. A great many trees, when growing under conditions that make them produce long flaccid branches, show a tendency to become passively weeping trees, e.g. species of *Fagus*, *Tilia*, *Fraxinus*, *Salix*, and many others.

The ultimate position taken up by the branches is the result of several concomitant causes, partly external, such as weight, and in a less degree light, and partly internal. The direction taken by the branch in many Phanerophytes is determined partly by its vegetative strength, so that the more vigorous the branches are the more acute is the angle they subtend to the mother shoot, and the more they follow the direction of the mother shoot. For example on vigorous shoots of *Prunus spinosa* the lower and middle buds grow out into short thorn-tipped branches which subtend approximately a right angle with the mother axis, whether the mother axis itself is placed vertically or obliquely. Only a few of the upper buds form long shoots, and these arise at an acute angle. *Prunus Padus* and *Rhamnus catharticus* behave in the same way. In the latter the short branches, which are often thorn-tipped, are frequently curved towards the base of the mother axis, while the upper ones arise at an acute angle.

Internal causes which influence the direction of the twigs operate only when the buds develop into shoots the same year they are laid down, or the year after. The direction of branches which arise two or more years after the formation of the mother shoots seems to be determined almost exclusively by weight. Under certain circumstances light may also influence the direction. Such shoots are therefore nearly always vertical or approximately vertical, whatever the direction of the mother shoots may be. A familiar example of this is the shoot from the stool. Many Phanerophytes produce now and again from older branches new vigorous shoots which, without regard to the direction of the mother shoot, ascend vertically into the air. Weak lateral illumination will cause these branches to rise obliquely. Such shoots are frequently seen in the following genera: *Prunus*, *Pyrus*, *Crataegus*, *Platanus*, *Diervillea*, *Lonicera*, *Viburnum*, *Sambucus*, *Philadelphus*, *Deutzia*, *Fraxinus*, *Ligustrum*, *Hippophaë*, *Elaeagnus*, *Catalpa*, *Ribes*, and many others.

Here it may be mentioned that the direction of suckers, as is well known, is determined by gravity. Suckers are markedly negatively geotropic.

Thus we see in Phanerophytes all possible gradations in the influence exerted by geotropism on the direction of the shoot. The direction of the primary shoot, which of course has no mother shoot, apart from the effects of illumination, is usually exclusively determined by the negative geotropism of the shoot. Primary shoots are negatively geotropic, as

also are suckers and late shoots. By late shoots I mean those that grow out from mother shoots two or three years old. The direction of ordinary side shoots which grow out from annual mother shoots is on the contrary influenced to a less extent by geotropism; in these internal causes play the principal part.

It is a well-known fact which has already been touched upon that the weight of the twigs of Phanerophytes plays an important role in determining their direction. Especially in individuals which stand free, or nearly so, the branch system may become entirely pendulous, though the young shoots may curve upwards so that the system becomes more or less 'S' shaped. It seems to me that the condition of affairs in markedly weeping trees is somewhat different. In these the branches hang down more vertically and the young shoots are not curved upwards at the apex, as always happens in plants whose shoots are negatively geotropic and at the same time not sufficiently rigid to remain erect for their whole length nor to maintain a definite direction. Many physiologists (Hofmeister, Frank, Voechting, Baranetzky, &c.) think that the branches of the pendulous Ash and pendulous Elm hang by their own weight. According to Baranetzky the shoots of these trees are really negatively geotropic, but as the pendulous varieties have longer and weaker internodes than the type species, the negative geotropism is held in abeyance. Of these forms I have had an opportunity of observing only the pendulous Ash, whose shoots are certainly weak, but that they are so weak that they have not even the power to show a slight negatively geotropic bend, if they are really negatively geotropic, in a short portion of their distal ends seems to me improbable. I have, however, carried out no experiments with these forms, but I have done so with a few corresponding trees such as *Betula alba* var. *pendula* and *Sambucus nigra* var. *pendula*.

I do not know how the branch system of *Betula alba* var. *pendula* initiates its weeping habit; presumably it occurs passively; but when the branches have at last taken up a pendulous position, apparently the direction of the lateral shoots is not affected by geotropism; these grow obliquely downwards, forming a rather definite angle with the mother shoot. In their growing apices we see no kind of negatively geotropic turning upwards, although they are sufficiently rigid, at any rate in a short length, to maintain an obliquely erect position. If a twig be placed so that its apical shoot points obliquely upwards, it always remains for a long time in that position; it seems, therefore, remarkable that if they are really negatively geotropic they should not show the same upward curve shown by negatively geotropic plants which have weak, and therefore procumbent pendulous twigs, and exhibited by all other negatively geotropic plants. And, even if it should turn out, in conformity with Baranetzky's experiments on Elms, that the shoot-apices bend upwards in pendulous Birches and other weeping trees when the leaves

are removed from the shoots, it cannot from that fact alone be concluded that it is weight that makes shoots droop, because to deprive a shoot of leaves is to make a profound disturbance in its economy and all the phenomena which depend upon its economy. It is as reasonable to suppose that the altered direction of the shoot when the leaves are removed is brought about by the removal of the leaves causing an alteration of the shoot's geotropism, as is the supposition that a negative geotropism, which is present before the removal of the leaves, is first able to make the shoot bend upwards when it is relieved of their weight.

Sambucus nigra var. *pendula* has its twigs directed vertically downwards. Both in light and darkness, and when the mother shoots are placed vertically with the apices pointing either upwards or downwards, the lateral shoots grow downwards. At length the shoots reach the ground and are compelled then to grow horizontally. If the youngest part of such a shoot be fastened so that its apex is turned upwards it then bends down, and the curve it makes does not give the impression of being brought about solely by the weight of the shoot, for the shoot apex is sufficiently rigid to stand vertically or horizontally.

Now whether the shoots of *Sambucus nigra* var. *pendula* become drooping, and at length procumbent on the ground, because their reaction towards gravity is different from that which obtains in ordinary Phanerophytes, or whether they behave in this way because of their own weight, we have in either case, within the same species, an interesting transition between the Phanerophytes and the Chamaephytes; for while the type *Sambucus nigra* is a marked Phanerophyte, var. *pendula* is a Chamaephyte, whose shoots lie horizontally on the ground.

Such a change in the shoot's reaction towards gravity occasioning a transition from Phanerophyte to Chamaephyte is met with in many genera, so that some species within an individual genus have negatively geotropic shoots, and are therefore Phanerophytes, while other species whose shoots grow approximately at right angles to the gravitational pull are Chamaephytes. Examples may be seen in *Salix* and *Rosa*.

Phanerophytes include a long series of gradations in their adaptation. We therefore see that although Phanerophytes are predominantly plants of favourable climates, yet they are found in many other regions; only from the most unfavourable of all climates are they entirely excluded. The vast majority of Phanerophytes are indigenous in tropical and subtropical regions, where there is not an excessively long dry season.

The causes which have enabled comparatively few Phanerophytes to extend beyond the boundary of the warmer parts of the earth are presumably various; some of these causes are not yet understood. Apart from the question of water it is certain that the reduction in tempera-

ture is the most important cause. Different species of plants are able to endure during the resting season different degrees of cold, that is to say, a difference in the lowness of temperature both maximal and total, and they demand a difference in the height of the temperature in the vegetative season; but however the matter stands for individual species it is quite certain that the Phanerophyte is the type of plant which belongs properly to the warmer and comparatively moist regions of the earth, and that comparatively few species of Phanerophytes have become
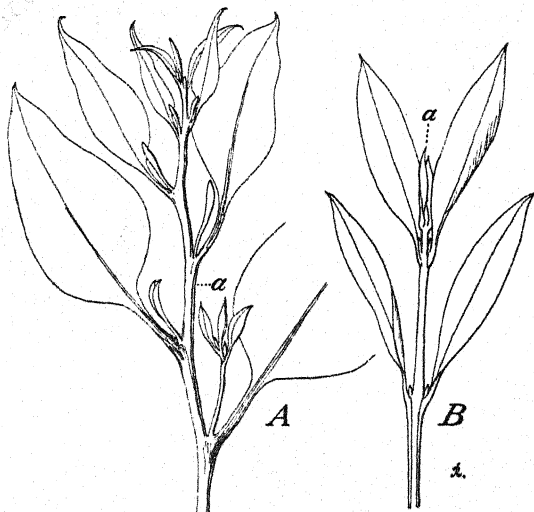

Fig. 8. Phanerophytes without bud-covering. A, *Eucalyptus orientalis*, the top part of a shoot; *a*, the line of demarcation between two periods of growth (⅔ nat. size). B, *Olea europaea*, a shooting twig; *a*, the leaves of the latest period of growth, which are about to grow out (nat. size).

adapted to life in colder climates. It is true that we have in the temperate, fairly humid regions large areas with Phanerophytic vegetation, such as the extensive woodland formation of the temperate zones; but this Phanerophytic formation is made up of comparatively few species, and that they are rich in individuals obviously does not invalidate the statement that the Phanerophyte is the plant type that belongs to warm regions; it only shows that those species which have become adapted to life in less favourable climates are specialized.

We must now try to discover and describe the characters of a series of sub-types of Phanerophytes which will be useful to us. Here we meet, as we always do in this domain of investigation, the great difficulty that the degree of adaptation cannot be determined by merely looking at the plant; while the sub-types in order to be useful to us must be recognized at sight. Our difficulty is that the protection of the growing point against the effects of the unfavourable season can take place in

many ways, and we are often unable to determine the efficiency of the protection afforded.

The growing point may be protected directly by bud-scales, or the protection may be indirect. Indirect protection is of four kinds. Firstly, the foliage may be thrown off at the onset of the unfavourable season.
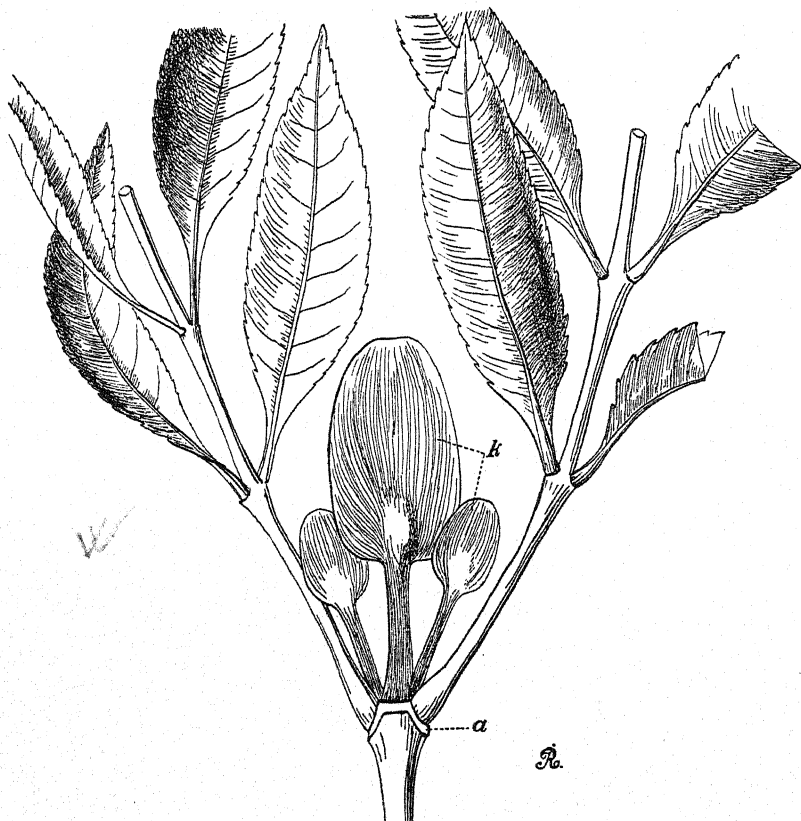

FIG. 9. *Cunonia capensis.* The unexpanded leaves are entirely enclosed by the large interpetiolar stipules (*k*) whose margins are firmly united (¾).

Secondly, the plant may be reduced in size, so that the shoot apices or buds are not so exposed to desiccation. This adaptation is of course especially efficacious in Phanerophytes which grow beneath taller Phanerophytes. Thirdly, the plant may be anatomically xerophilous, so that its whole structure is protected against drought: the growing points, of course, participate in this protection. Fourthly, the actual structure of the cells may be drought-proof (intracellular xerophily). The order in which these five adaptations are mentioned correspond essentially with their usefulness in establishing sub-types.

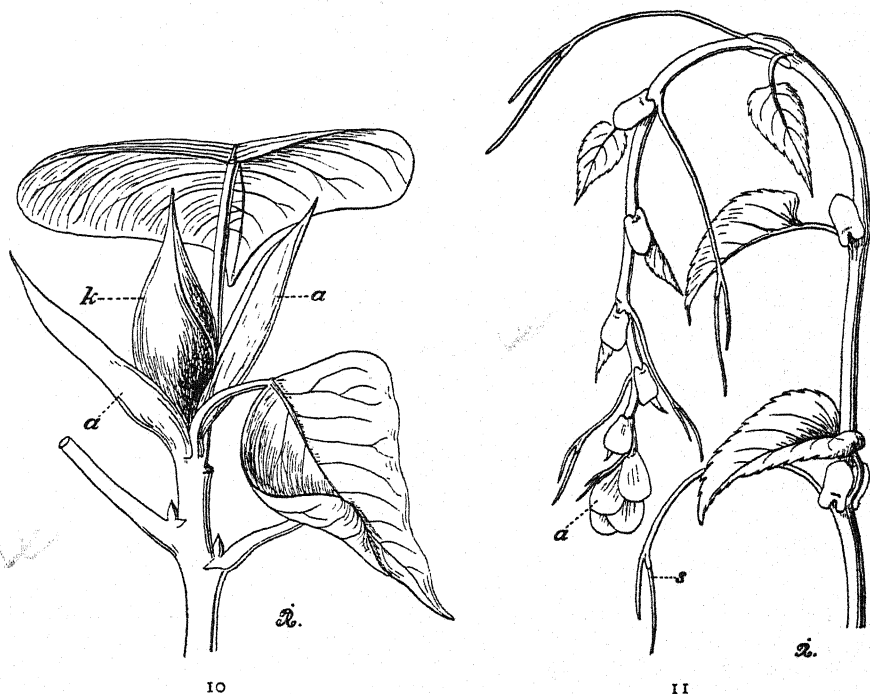Bud-covering. We can divide Phanerophytes into two groups;

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FIG. 10. *Homalanthus Leschenaultiana.* The leaves become very large before they unfold, and remain enclosed and protected by the balloon-shaped stipules of the latest developed leaves, *k*. (⅟₁)

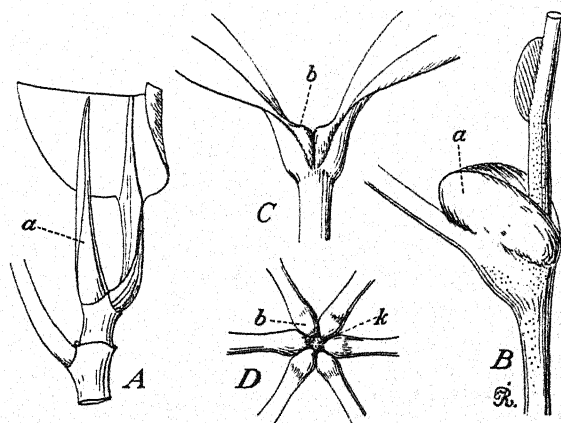FIG. 11. *Cissus* sp. The young leaves are protected by stipules, *a*. (⅟₁)

FIG. 12. Examples of evergreen Phanerophytes whose shoot apices with their young leaves are protected by the already developed foliage leaves. A, *Ficus rubiginosa*; *a*, the ligule of the last developed leaf, which fits like a cap over the shoot apex. (¾). B, *Leea sambucina*; *a*, the large stipules of the latest developed leaf surround the apex of the shoot, which is now about to sprout. (¾). C, *Fagraea zeylanica*; the shoot apex is protected by the expanded bases of the latest developed leaves. These leaf-bases are closely applied to each other, *b*. (¾). D, *Allamanda verticillata*; the shoot apex, *k*, is protected by an expansion, *b*, at the base of each leaf of the last developed whorl. (¾)

Phanerophytes without bud-protection (Fig. 8) and Phanerophytes with bud-covering. The boundary however between these two groups is not as definite as one might at first suppose.

The Phanerophytes which grow in constantly warm and constantly moist regions are less protected than any others. They show no visible signs of bud protection; their buds are, as a rule, very small and consist of but few leaves, in the development of which there is no perceptible pause.

But as soon as we come to regions which have a dry period, though it may be only a short one, we meet with Phanerophytes whose leaf primordia are protected in various ways. Some have their young, still unfolded leaves covered with hairs, or surrounded by hairs springing from neighbouring parts of the plant. Others have a covering of mucilage, and others again are protected by the stipules, which either belong to undeveloped leaves, *Cunonia capensis* (Fig. 9), *Homalanthus Leschenaultiana* (Fig. 10), species of *Cissus* (Fig. 11), *Leea* (Fig. 12, B), *Coprosma*, &c., or the stipules may belong to leaves which are already developed, e.g. *Ficus* sp. (Fig. 12, A), or the shoot apex with the leaf primordia may be surrounded and protected by the base of the already developed leaf (*Fagraea zeylanica*, Fig. 12, C, and *Allamanda verticillata*, Fig. 12, D).
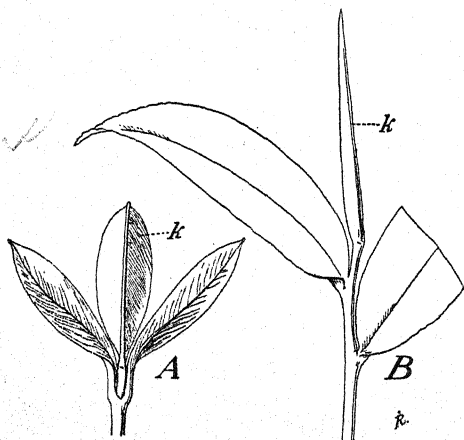

FIG. 13. Phanerophytes without bud-scales. The leaves grow nearly to their full extent before they unfold. The younger leaves are protected for a long time by the older ones. A, *Veronica elliptica*. (¼). B, *Marcgravia* sp. (⅔); *k*, still unexpanded leaves.

All plants have their young leaves protected for a longer or shorter period by the older leaves. In many Phanerophytes which have no bud-scales this protection is very noticeable because the leaves attain a considerable size, they become in fact almost full grown, before they unfold, and continue for a long time to enclose the younger leaves, which thus develop considerably before they suffer any direct exposure to the desiccating air. Examples of this are seen in many evergreen species of *Veronica*, e.g. *V. elliptica* (Fig. 13, A), *V. salicifolia*, *V. Kirkii*, *V. Traversii*, *V. speciosa*, *V. parviflora*, &c. Further examples are *Marcgravia* (Fig. 13, B) and *Melaleuca*, e.g. *Melaleuca hypericifolia* and *M. violacea*. In some plants the margins of the leaves which surround the apex adhere together, or they are held together by hairs, e.g. *Veronica elliptica* and *V. salicifolia*. In some species the space enclosed by the

outermost leaves is completely packed with young leaves, e.g. *Veronica parviflora* and *V. Traversii*; in others there are much fewer young leaves, and the space is partially filled with fluid, e.g. *Veronica salicifolia*.
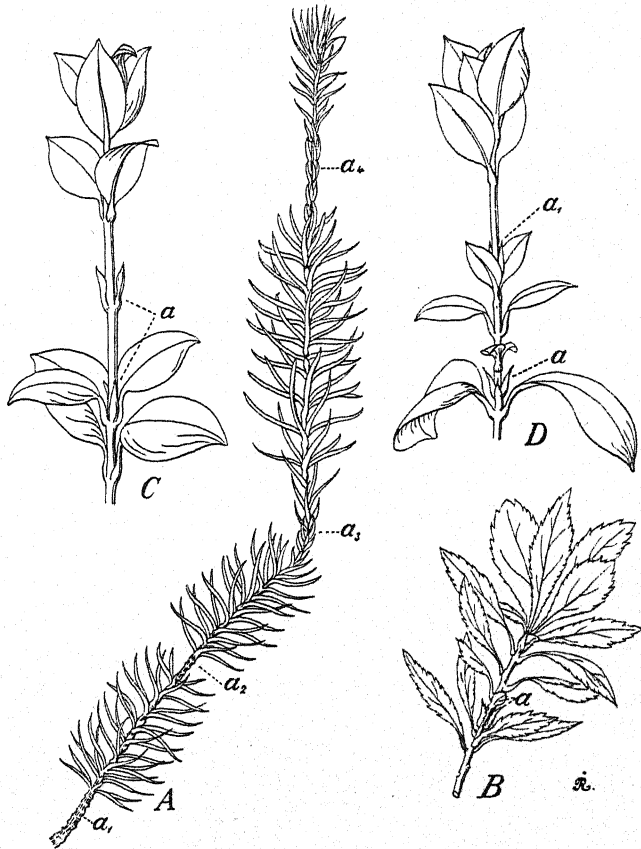

FIG. 14. Examples of the transition between foliage leaves and bud-scales in evergreen Phanerophytes. A, *Erica multiflora*; four-year-old branch with foliage leaves separated by sets of less developed leaves, *a*, which are however proper foliage leaves, that have developed at the beginning of the unfavourable season and have served as a protection for the young unexpanded foliage leaves; these protective leaves are influenced by the unfavourable season in such a way that they are not able to continue their development further when the favourable season begins; they are smaller and more erect than the real foliage leaves and fall off sooner, a_1 and a_2. (‡). B, *Escallonia rubra*; branch with transitional leaves, *a*, between two sets of leaves belonging to periods of growth (‡). C and D, *Myrtus ugni*; branch with transitional leaves, *a*, between two sets of ordinary leaves; a_1 (in D), transitional leaves which indicate a temporary pause in development during the last period of growth. (⅘)

A somewhat similar protection is seen in a large number of evergreen small-leaved Phanerophytes, chiefly Nanophanerophytes, which have at the ends of their stems a great many young leaves in different stages of development. These are surrounded and protected by older leaves until they are full grown. Examples are: *Calluna vulgaris, Pentapera sicula,*

Fabiana imbricata, Calocephalus Brownii, Diosma oppositifolia, Aga-thosma apiculata, Phylica ericoides, Melaleuca armillaris, species of *Erica* (Fig. 14, A), *Gnidia* and many others.

Finally we have numerous species in which the protection takes place by real bud-scales, that is to say by leaves whose function is exclusively protective.

Now it is probable that buds which are protected by the stipules or
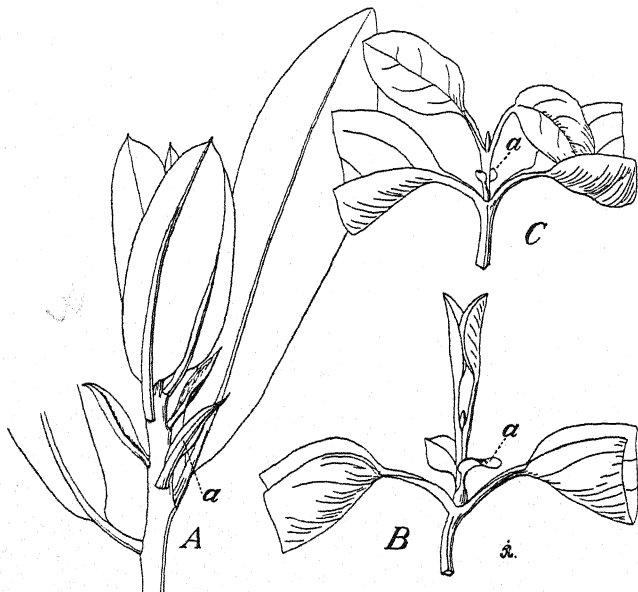

FIG. 15. Evergreen Phanerophytes which show the transition to real bud-scales. A, *Drimys Winteri*; *a*, undeveloped leaves which have served as a protection for the young foliage leaves during the unfavourable season. (⅔). B and C, *Viburnum tinus*; shoot with more or less reduced transitional leaves, *a*, between those belonging to two periods of growth. (⅘)

leaf-bases of ordinary foliage leaves are just as well protected as those furnished with bud-scales. For example, the young leaves of *Cunonia* are very efficiently protected by the unexpanded adherent stipules. *Homalanthus Leschenaultiana, Ficus, Philodendron,* &c., are other examples of efficient protection without the aid of bud-scales. In spite of this fact, however, I have deemed it fitter to draw the boundary between the two groups according to whether proper bud-scales, as defined above, are present or absent. Where there are real bud-scales (Figs. 17, 18 and 19) the climatic periodicity is expressed by a corresponding morphological periodicity, which is easily observed and which is therefore of practical use to us in our classification. Those plants which, according to this division, come under the category of those without proper bud-scales, but whose growing points are well protected, whether by stipules, leaf-

bases, or any other such means, might if desired be made into a group by themselves.

The boundary between plants with bud-scales and those without is not a sharp one; there are a number of Phanerophytes without well-marked bud-scales which have, however, a morphological periodicity dependent on the climate. At the beginning of the unfavourable season they form
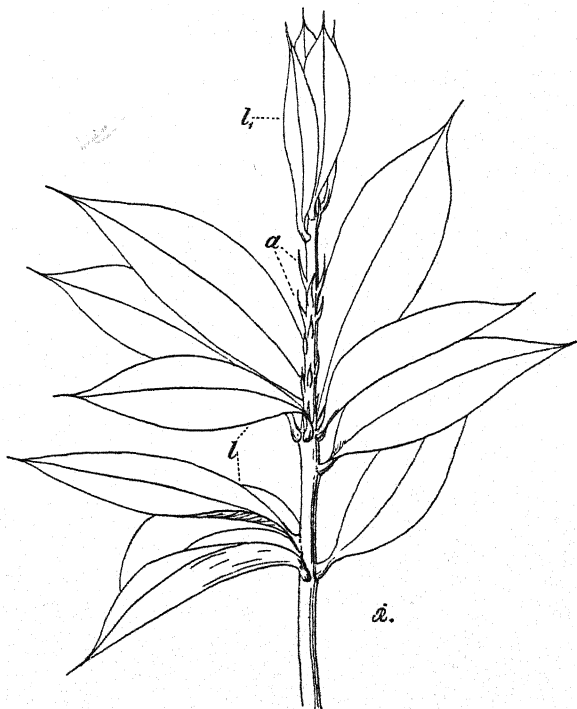

FIG. 16. *Jacquinia acuminata* sprouting; *a*, the bud-scales are separated by distinct internodes so that the young foliage leaves, l_1, are borne above the older ones, l. ($\frac{2}{3}$)

leaves which are indeed green, and on the whole resemble foliage leaves, but never attain their full size. They remain small, and the internodes which separate them elongate but little; when the favourable season comes they have so far completed their structure that they are not able to grow any more. These leaves without having the special structure of bud-scales serve to protect the younger unexpanded leaves during the unfavourable season. As examples may be mentioned *Escallonia rubra* (Fig. 14, B), *Myrtus ugni* (Fig. 14, C and D), *Drimys Winteri* (Fig. 15, A), and *Viburnum tinus* (Fig. 15, B).

We find a second more advanced transition in plants which indeed have bud-scales, in that the protecting leaves always remain scale-like, but the internodes between these leaves elongate to a greater or lesser

extent when the shoot develops. By this means the assimilating part of the shoot is borne farther away from the mother shoot; examples *Jambosa australis, Carapa procera, Eriodendron anfractuosum, Jacquinia acuminata* (Fig. 16) and *J. aurantiaca*.

Making use of leaf-fall and bud-covering as characters we obtain at once three obvious and useful types: (1) Evergreen Phanerophytes without bud-covering, (2) Evergreen Phanerophytes with bud-covering, and (3) Deciduous Phanerophytes with bud-covering. The distribution of these three types is on the whole closely correlated with the changes experienced in passing from constantly warm and humid tropical climates, through tropical and sub-tropical regions with a rainy and a dry season, to the colder parts of the earth, where there are long and more or less severe winters.

If we examine more closely the behaviour of these types within their regions of distribution, it becomes obvious that gradually, as the unfavourable season becomes longer and more severe towards the boundaries of the areas of the types, the plants become lower and lower. Gradually, as one departs from the coastal regions with tropical forest to regions farther inland where the dry season becomes longer and more severe, the woods become progressively lower. Similarly, in the colder regions of the earth the nearer we approach the poles, or the higher we climb into the mountains, the stature of the Phanerophytic vegetation dwindles, till at last it becomes composed entirely of Nano-

FIG. 17. *Griselinia litoralis* Raool. Evergreen Phanerophyte with bud-covering formed of one to several bud-scales. a_1, bud-scales on the boundary between this year's and last year's growth, a, scar of the corresponding bud-scale between growth period of last year and the year before. Side shoots (*s*) have appeared a little above their axillant leaves. ($\frac{2}{3}$)

phanerophytes, which, by their lowness, have the advantage of being protected during the winter by snow, and by that means alone are able to survive the unfavourable season. Now dwarf growth (nanism), as understood here, has often perhaps not arisen as an adaptation for surviving the unfavourable season, but is probably a direct result of all the unfavourable

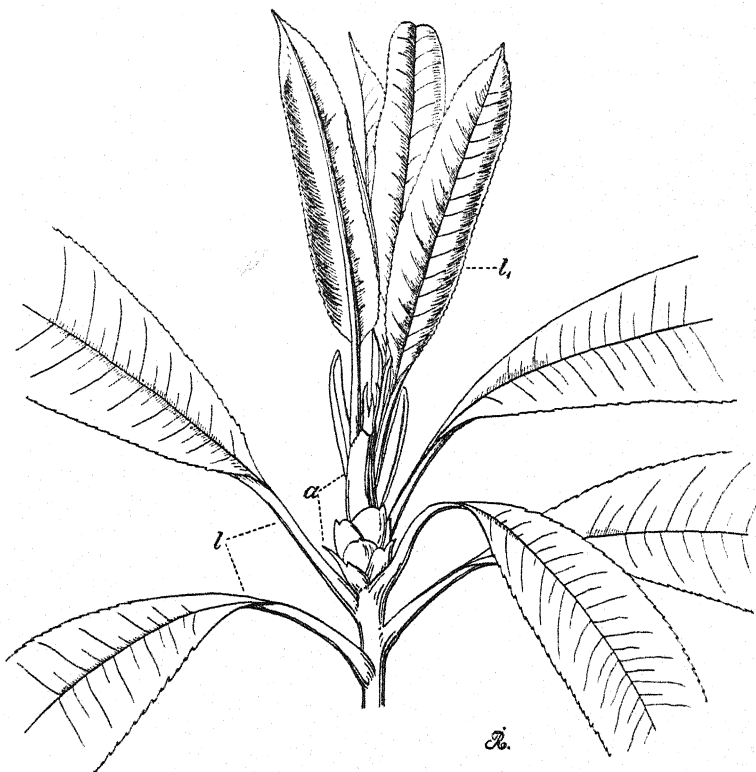Fig. 18. *Photinia serrulata* sprouting; *a*, Bud-scales. ($\frac{2}{3}$)
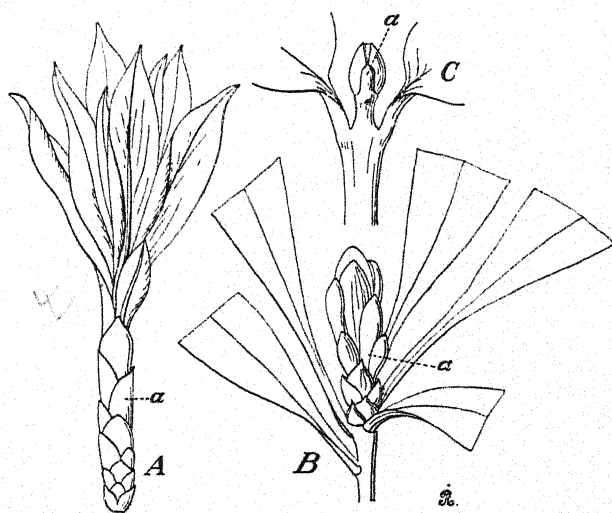

Fig. 19. Evergreen Phanerophytes with bud-coverings, *a*. A, *Pittosporum undulatum.* ($\frac{1}{1}$). B, *Pittosporum crassifolium.* C, *Metrosideros tomentosa.* ($\frac{2}{3}$)

factors; but on the other hand dwarf growth is certainly an advantage to the plant that is obliged to survive unfavourable seasons, and since this character is very useful to us, it is convenient to subdivide the three above-mentioned types according to their size. Investigations in the field must decide how many divisions according to size it is useful to make, and at what height the boundary between them must be drawn. According to my experience it is useful to make four classes within each of the already mentioned types of Phanerophytes. In descriptions of Phanerophytic vegetation the specification of height is often left out; and the absence of the information makes our task a difficult one. I shall attempt it however by making use partly of what I have seen, and partly of what I have read. If the results thus obtained do not lead to the establishment of useful boundaries between heights, we must of course employ other methods. Our results must accommodate themselves to the picture of vegetation as a whole, and not to the vegetation of one particular region.

According to my own knowledge and according to the scanty information about the height of Phanerophytic vegetation in different regions which I have culled from literature, I assume that the boundaries between the four chief types can be drawn at 2, 8, and 30 metres, thus:

Nanophanerophytes	.	.	.	. under 2 metres
Microphanerophytes	.	.	.	. 2–8 ,,
Mesophanerophytes	.	.	.	. 8–30 ,,
Megaphanerophytes	.	.	.	. over 30 ,,

Various causes co-operate in occasioning the transition from Mega-phanerophytes to Meso-, Micro-, and Nano-phanerophytes. We must consider especially the impoverishment of the environment brought about partially by increasing length and severity of the dry period, partially by increasing length and severity of the period of cold, which indeed has the same effect on plants as drought, and partially also by the decrease in available nourishment caused by poorness of soil. But whatever the causes may be, the plants by diminishing their size gain an advantage in surviving the unfavourable season; they are better protected against drought.

The two last of the five adaptations mentioned on page 24, anatomical and intracellular xerophily, are not useful characters in making types, but we may of course employ these characters for further demarcation of sub-types which have been separated off by other means.

Considering bud-covering and leaf-fall in connexion with the four above-mentioned classes, we obtain twelve sub-types within the Phanero-phytes; further we get three types peculiarly easy to recognize: (1) Phanerophytic Herbs, (2) Phanerophytic epiphytes, (3) Phanerophytic stem-succulents.

Herbaceous Phanerophytes. Under this heading I include the vast number of Phanerophytes, more or less herbaceous, and found especially in regions with an almost constantly humid tropical climate. They resemble our large herbs, but their aerial shoots remain alive for several years without becoming woody; their stems are as a rule weaker than in real woody plants; strengthening tissue is not so much developed, and there is comparatively more parenchyma than there is in woody plants. Because of their lighter herbaceous structure herbaceous Phanerophytes are the least protected of all Phanerophytes; they are therefore found particularly in the most favourable climates, where they live for the most part protected by the higher Phanerophytic vegetation. As examples can be named: *Scaevola Koenigii*, *Rhytidophyllum tomentosum*, *Myriocarpa macrophylla* and other *Urticaceae*, species of *Impatiens*, many Begonias, *Acalypha hispida*; and many other *Euphorbiaceae*, species of *Piperaceae*, *Phytolaccaceae*, *Acanthaceae*, *Labiatae*, *Compositae*, *Verbenaceae*, *Araceae*, *Commelinaceae*, and other families.

As long as the concept of the herbaceous Phanerophyte is omitted by students of floras, we shall have to refer plants belonging to this category to the above-mentioned classes which are demarcated by size; most of them will be included among the Nanophanerophytes; but the importance of attempting to separate herbaceous Phanerophytes from Nanophanerophytes is apparent from the fact that while Nanophanerophytes (and Chamaephytes) characterize the tropical and the sub-tropical regions with a marked, but not an excessively severe, dry period, the herbaceous Phanerophytes, on the other hand, belong to types characteristic of constantly warm and constantly moist tropical climates.

In regions with a well-marked dry season the type of herbaceous Phanerophyte passes imperceptibly into the Chamaephyte, especially into the suffruticose Chamaephyte; because in this type the upper parts of the shoot die in the unfavourable season, leaving only the lowest part of the shoots with the buds attached to them to survive the unfavourable season. From the suffruticose Chamaephyte development, or rather reduction, proceeds as far as the Protohemicryptophyte.

The two other types, stem-succulent Phanerophytes, which have succulent stems without proper foliage leaves, and Epiphytic Phanerophytes (under this heading we must reckon also the Phanerophytic parasites), need no further description. They are characteristic of certain definite climates, and as they are easy to separate from other Phanerophytes they therefore form useful types.

Conspectus of Phanerophytic Sub-types. Within the Phanerophytes we have thus the following fifteen sub-types:

1. Herbaceous Phanerophytes
2. Evergreen Megaphanerophytes without bud-covering
3.   ,,   Mesophanerophytes   ,,   ,,

   4. Evergreen Microphanerophytes without bud-covering
   5.   ,,   Nanophanerophytes   ,,   ,,
   6. Epiphytic Phanerophytes
   7. Evergreen Megaphanerophytes with bud-covering
   8.   ,,   Mesophanerophytes   ,,   ,,
   9.   ,,   Microphanerophytes ,,   ,,
  10.   ,,   Nanophanerophytes   ,,   ,,
  11. Stem-succulent Phanerophytes
  12. Deciduous Megaphanerophytes   ,,   ,,
  13.   ,,   Mesophanerophytes   ,,   ,,
  14.   ,,   Microphanerophytes ,,   ,,
  15.   ,,   Nanophanerophytes   ,,   ,,

We have here, of course, no continuous series in the sense that each member is better adapted than the one before to survive the unfavourable season. This, however, shows no defect in the types; it is, on the other hand, a natural expression of the fact that climate-forms do not constitute one, but several series. It is in harmony with this fact that there are no sharp boundaries between the types; the same species passing from one climate to another often changes its type; species which in a more favourable climate are Evergreen Phanerophytes may in a less favourable climate occur as Deciduous Phanerophytes; species which in certain climates are Microphanerophytes very often become in more unfavourable climates Nanophanerophytes. This is, as already said, not a defect in the types, but on the other hand a merit, for it shows that the types are in harmony with nature: with a change in climate there occurs a corresponding change in life-form, which is indeed an expression of the climate.

II. Chamaephytes

By Chamaephytes I mean plants whose buds or shoot-apices destined to survive the unfavourable season are situated on shoots or portions of shoots which either lie on the surface of the earth or are situated quite near to it, so that in regions where the ground in winter is covered with snow this can protect them, or in warmer regions with a dry season the buds can be partially protected by the withered remains of the plants on the surface of the ground. In either case, because the buds of these plants are near the surface of the earth, they are *ceteris paribus* much better protected than the buds of Phanerophytes, which are situated on shoots projecting a long way into the atmosphere.

The flowering shoots are, as a rule, negatively geotropic, and project freely into the air; they live only during the favourable season, and have to occupy a conspicuous position to ensure pollination, whether by animals or by the wind.

On the other hand the persistent shoots which bear the surviving buds

lie along the earth, or at any rate do not project more than 20 or 30 cm. above it. If they project to a greater height the plants pass into the category of Phanerophytes. Different causes determine the proximity of the shoots to the ground in different Chamaephytes, and the greater or less degree of adaptation to life near the ground can be used for making divisions within the type.

In some Chamaephytes the shoots that bear the surviving buds are near the ground, because the shoots, which project into the air in the favourable season, die back to near the ground at the beginning of the unfavourable season. I call this type Suffruticose Chamaephytes. In others the shoots lie on the ground because of their weight; these shoots are long, slender, and comparatively flaccid, and plants possessing them I call Passive Chamaephytes. The most pronounced Chamaephytes lay their shoots flat on the ground because their shoots are transversely geotropic, i.e. they take up a horizontal position in response to the action of gravity. Plants possessing such shoots I call Active Chamaephytes; they are the most marked of all Chamaephytes because they have become Chamaephytes by an alteration of the physiological reaction of their shoots, the reaction towards gravity. Cushion Plants constitute a fourth type, forming a transition to the Hemicryptophytes. In Cushion plants the surviving buds or shoot-apices are close to the ground because the shoots are very low; they are, as a rule, so closely packed together that they both support and protect one another.

16. **Suffruticose Chamaephytes.** The shoots which develop in the favourable season are as a rule markedly negatively geotropic and bear leaves and flowers. At the end of the vegetative period the upper parts of these shoots die away so that only the lower portions survive the unfavourable season, and these surviving portions bear the buds which in the next period of growth are destined to grow out into shoots bearing leaves and flowers (Fig. 7, 2). This proximity of the buds to the ground saves them from being exposed to the desiccation to which the buds of Phanerophytes are exposed. The buds of the Suffruticose Chamaephytes are in part protected from desiccation by the wholly or partially dead plant-remains which lie on the surface of the ground.

The length of the persistent portion of the shoot varies widely, and in individual species is to a certain extent adapted to the climate. If the conditions are particularly favourable it is only the most distal portions of the shoots that die, and the plants then often very closely resemble Herbaceous Phanerophytes, from which type they have certainly been in great part derived. If the conditions are very unfavourable then the shoots die back nearly to the ground, forming imperceptible gradations towards the first type of Hemicryptophytes. Nanophanerophytes also often make transitions to Suffruticose Chamaephytes. The fact that the spaces between the life-forms are thus bridged within

a single species when the unfavourable season is more severe, shows that the plan on which the life-forms are built is able to reflect with accuracy changes in climate; this indeed is its chief task.

Suffruticose Chamaephytes are doubtless especially widely distributed in the warm and warm-temperate regions of the earth with a rather long dry season, where the factors are less favourable than in the regions where Nanophanerophytes have the upper hand; but the two types often grow together. Suffruticose Chamaephytes are especially in evidence in many parts of the Mediterranean region, where they are represented by species of *Labiatae, Caryophyllaceae, Leguminosae,* and other families.
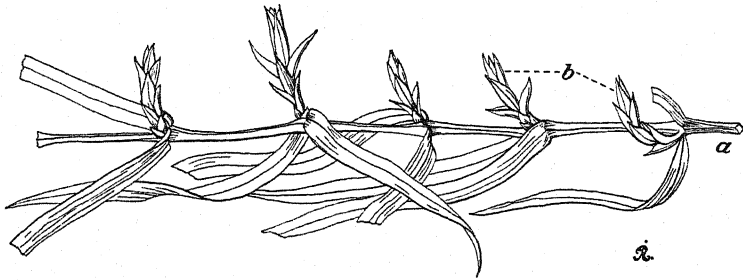

FIG. 20. *Stellaria holostea;* detached portion of an aerial procumbent shoot, *a,* from whose leaf-axils the buds, *b,* destined to survive the winter, are shooting.

In this sub-type I include also a small group of Chamaephytes whose shoots are upright and negatively geotropic but always of meagre stature. Their shoot-apices do not die like those of the real Suffruticose Chamaephytes; but these plants cannot be included among the Cushion plants because they form no cushions.

17. **Passive Chamaephytes.** The vegetative shoots are, like those of Phanerophytes, negatively geotropic and persistent, remaining intact at the beginning of the unfavourable season; but because they are weak in proportion to their length and not furnished with sufficient strengthening tissue, they are not able to stand erect, but fall over and lie along the ground. It is only the apices of these shoots that are erect or ascending, because it is only at the apex that the negative geotropism is able to influence growth; the extent of this influence depends upon the rigidity of the shoot. By observing the growing apices we can easily determine whether the plant is a passive or an active Chamaephyte; if it is active even the growing apices are horizontal. Among passive Chamaephytes we find evergreen and deciduous species, species with and species without bud-covering. Some are pronounced woody plants, others more herbaceous. These and other characters can guide us in making sub-types. They all belong especially to the Alpine region.

Examples are: *Arabis albida, A. alpina, Aubrietia* sp., *Veronica* sp.,

Sedum, Saxifraga, Polygonum brunonis, Kernera saxatilis, Stellaria holostea (Fig. 20), *Cerastium tomentosum, C. trigynum*, and several other species of *Cerastium, Campanula fragilis, Lotus peliorrhynchus*, and many others.

18. **Active Chamaephytes.** These too have persistent vegetative aerial shoots, but they differ from the Passive Chamaephytes, in that the shoots lie along the ground because they have a different reaction towards gravity, pursuing a direction at right angles to the gravitational pull (transverse geotropism) (Fig. 7, 3). The growing apices therefore do not ascend like those of the Passive Chamaephytes, though they sometimes appear to do so from the leaves being bent upwards. Sometimes the shoots lie on the ground because they are negatively heliotropic.

This type, like the last, contains both evergreen and deciduous species, some with and some without bud-covering; some are pronounced woody plants, others herbaceous. As shoots which lie on the ground are inclined to strike root when they come into contact with damp earth, this type passes by imperceptible gradations into Hemicryptophytes with aerial stolons. The difference between the two types depends upon whether or not the roots draw the surviving buds down into the soil. Unless this takes place throughout a long series of buds, I include the plant among the Hemicryptophytes. Because of the nature of the case we should not, and indeed cannot, draw a sharp boundary.

Examples of Active Chamaephytes are: *Thymus* sp. (e.g. *Thymus zygis*), *Veronica officinalis, Vinca, Acaena Novae Zealandiae, Cerastium caespitosum, Arctostaphylos uva ursi, Empetrum nigrum, Linnaea borealis, Lysimachia nummularia*, and many others.

Looked at biologically the Active and the Passive Chamaephytes are essentially the same, and their occurrence points to approximately the same conditions. They differ chiefly in the physiological method by which they have become Chamaephytes: the Active Chamaephytes have adopted the more thorough method, so this type may be looked upon as the more perfectly adapted of the two. Both types are specially constructed to live where there is a snow covering which protects the shoots and buds against loss of water; they are both comparatively abundant in alpine regions.

If the shoot of an Active Chamaephyte be fixed in the light with the apex pointing upwards, when growth continues it will bend again in a horizontal or obliquely descending direction, and go on growing until the shoot, partly or entirely of its own weight, reaches the surface of the ground, and then grows along it. On the other hand in the dark the shoots of these plants are negatively geotropic, at any rate in the species I have investigated, e.g. *Cerastium caespitosum, Veronica officinalis*, and *Lysimachia nummularia*. The behaviour of *Lysimachia* has already been discussed by Oltmanns, and *Vinca major* behaves according to Czapek in the same way. In the three species mentioned above, *Cerastium*

caespitosum, *Veronica officinalis*, and *Lysimachia nummularia*, the shoots in my experiments showed themselves to be weakly positively heliotropic. In weak unilateral illumination they grew towards the light. Czapek has found that *Lysimachia nummularia* behaves in this way.

An interesting transition between Passive and Active Chamaephytes occurs in some species which seem to have entirely lost their sensitiveness to the stimulus of gravity. The shoots of these plants continue to grow in any direction in which they are placed; only the weight of the shoot forces it gradually out of that position, unless, of course, it has been placed with the apex pointing downwards. As in the Passive Chamaephyte the shoots of these plants rest on the ground because of their own weight, but they differ from the shoots of the Passive Chamaephyte in that the apices show no upward curving due to negative geotropism. On the other hand the horizontal direction of the shoot-apices is not, as in the Active Chamaephytes, determined by transverse geotropism, because the shoots are indifferent to gravity; their direction is due to the position their own weight has caused them to assume.

Rosa Wichuraiana is an example. This plant has procumbent shoots, which in the course of a season can grow several metres in length. The shoot-apices are sufficiently rigid to enable them to maintain a definite direction, at any rate for a short distance. This can be demonstrated by allowing a shoot lying on the ground to grow over a depression; the apex will grow on in its original direction without support; not until it is several centimetres long does its own weight begin to cause it to sink. Shoots fastened in a vertical direction with their apex upwards continue to grow upwards until they become so long that they lose their equilibrium and topple over by their own weight, which causes the shoots as they elongate to droop more and more until they become pendulous. Then growing vertically downwards they at last reach the earth, which compels them to grow to one side. Not even in darkness do the shoots of *Rosa Wichuraiana* appear to be negatively geotropic, as are many species with horizontal aerial shoots.

19. **Cushion Plants.** As in the Passive Chamaephytes the shoots are negatively geotropic, but arranged so close together that they prevent each other from falling over, even if they are not furnished with sufficient strengthening tissue to enable them to stand erect. The shoots, which are as a rule low, are often packed together so tightly that the cushion becomes quite solid. This solidity brings about a mutual protection to the shoots during the unfavourable season. The surviving shoot-apices are protected by withered leaves, as often happens in Hemicryptophytes. There are transitions between Cushion plants and the tussock-forming Hemicryptophytes. On the other hand Cushion plants are connected by imperceptible gradations to Passive Chamaephytes, from which they are certainly derived. A number of Passive Chamaephytes show a ten-

dency to form cushions. In favourable conditions the shoots are so lax that the branchlets are not pressed so tightly together as to support one another. Under these conditions a proper cushion is not formed. When, however, the conditions are less favourable the shoots are so short and arranged so close together that they become real cushion plants. Examples are seen in *Sedum, Saxifrage, Aubrietia,* and other genera.

Real Cushion plants belong, even more than the Passive Chamaephytes, to the alpine region. Examples are *Maja, Merope,* and *Azorella* in the Andes; *Myosotis Hookeri, Crepis glomerata, Saussurea hemisphaerica, S. gossypiphora, Acantholimon diapensioides,* and *Saxifraga hemisphaerica* in the highlands of Central Asia; *Myosotis uniflora, Veronica pulvinaris, Azorella elegans, Hectorella caespitosa, Raoulia mammillaris, R. eximia, R. australis,* and other spp. of *Raoulia, Haastia pulvinaris, H. Greenii,* and *Dracophyllum muscoides* in the mountains of New Zealand.

III. HEMICRYPTOPHYTES

This type is better adapted than the last to survive unfavourable seasons, the shoots dying back to the level of the ground at the beginning of the unfavourable period, so that only the lowest parts of the plant, protected by the soil and withered leaves, remain alive and bear buds destined in the next period of growth to form shoots bearing leaves and flowers (Fig. 7, 4). Thus in all Hemicryptophytes the shoot-apices which are to survive the unfavourable season are situated in the soil-surface, protected by the surrounding soil and by the withered remains of the plant itself.

In most Hemicryptophytes the surviving portion of the single shoot persists for several years, so that there is formed a more or less branched contracted system of shoot-bases corresponding to the shoot-bases of Suffruticose Chamaephytes, but differing from them in being situated in the ground and not above it.

Outside the warmer and the moderately humid regions of the earth, where Phanerophytes abound, the Hemicryptophytes are manifestly dominant; apart, that is to say, from the driest regions, where Crypto-phytes, and under certain conditions Therophytes, form an essential component of the vegetation. Most of our herbs are Hemicryptophytes, and probably about half of the plants belonging to Central Europe belong to this type.

Morphologically great diversity prevails in these plants, a diversity connected with the manifold devices for vegetative reproduction and distribution which often characterize Hemicryptophytes. They attain no great height, but spread extensively by means of horizontal runners. In some the primary root persists as it does in most Phanerophytes, and the whole shoot system lives as long as the individual; this type is

connected with the Suffruticose Chamaephytes. In most of them the primary root dies after a longer or shorter time and the individual becomes attached by adventitious roots. Not only does the primary root die, but the shoot system gradually dies back from behind, so that vegetative reproduction takes place by division, the individual parts of the shoot system becoming free by the dying of the older portions which held the younger together. The extreme in this direction is reached by those plants whose persisting shoot dies before the buds attached to it unfold. This, for example, may happen in *Epilobium montanum* (Fig. 21, B), *Samolus Valerandi*, species of *Aconitum*, &c. Persisting buds in these plants develop adventitious roots at a later stage, so that they are able to continue life independently.

The length of the persisting portion of the shoot varies greatly. If we confine ourselves first to those plants whose shoots are from the very beginning all negatively geotropic and therefore erect, then we find that the length of the persisting shoot depends upon the depth in the soil from which the shoot sprang, because the whole of the subterranean portion of the shoot, as a rule, remains alive, and only the aerial portion dies back. Normally the new shoots spring from the uppermost part of the persisting portion of the old ones, which are, of course, in the soil; but sometimes shoots arise lower down from dormant buds on portions of old stems. These buds have to break through a thicker layer of soil, so that their underground persistent portions are comparatively longer; but the buds destined to survive the unfavourable period and which in the next growing season are to form aerial shoots, are normally laid down in the portion of the shoots situated in the soil.

While the new shoots thus spring from that portion of the mother shoot which is in the soil, only the lowermost portion of these shoots remains covered by the soil; but that portion which is to bear the surviving buds must have a certain length even if its internodes are very short, and the plant's surviving shoot system will therefore ultimately grow up over the surface of the ground and die back if it has no other means of keeping itself covered. This protective covering is obtained in different ways, partly passively, partly actively. Passively it takes place, as is well known, by 'hilling', partly by means of worms and other animals, partly by the layer of dried plant-remains which every year is deposited on the ground. Actively the covering takes place by the contraction of the roots dragging the plant down into the soil; this has been shown to take place in many plants. By this means the underground stems are kept at such a depth that they are covered and the buds do not come above the surface of the ground.

It may however happen that the underground shoot system becomes buried too deeply. This may occur through the activity of moles or in other ways. Hemicryptophytes correct this state of affairs by laying

down their rejuvenating buds not at the base of the shoots but on the portion of the shoot which is in the upper layer of the soil; so that the surviving buds come to occupy the position characteristic of Hemi-cryptophytes.

Even if it be true that all Hemicryptophytes have their surviving buds or shoot-apices situated in the soil-surface, yet the various species belonging to this category are not all equally well protected, because there are also other means of protection than that afforded by the soil.

The side shoots which are laid down in the course of the favourable season and which are destined to develop in the following period of growth, always have some of the lowest leaves modified to be mainly protective. The degree of this protection varies widely, but it is difficult to measure, and is therefore unsuited to serve as a character for the formation of sub-types.

The apices of shoots which have already developed foliage leaves are as a rule not furnished with protective scales, but are protected by the lowermost portions of the living or withered leaves. This is well known in rosette plants. Only rarely does the shoot which has not yet formed an aerial portion, though it may possess radical foliage leaves, continue to the end of its period of growth to form scale leaves for protecting the apex: examples are *Carex caespitosa* and *C. stricta.*

The protection can thus be of various kinds. One must remember that there are also anatomical and intracellular adaptations; but as their degree is difficult to determine they cannot be used in classification, however tempting it may be so to use them. The sub-types within these life-forms will therefore be demarcated according to the degree in which the plant has been externally modified for its life in the soil, taking for granted that the ordinary aerial shoot is the most primitive.

As in Phanerophytes which have covered buds, the shoots of the Hemicryptophytes start with imperfectly formed leaves. Some Hemi-cryptophytes continue to produce imperfect leaves as far as the lowest part of the aerial shoot, on which are therefore found the largest foliage leaves and the greatest number. The part of the aerial shoot which has elongated internodes is the only flower-bearing and at the same time the only assimilating part of the plant; there is no radical rosette of leaves. This, the least altered type of Hemicryptophytes, I propose to call the Proto-Hemicryptophyte.

In other Hemicryptophytes, though the elongated portion of the aerial shoot bears foliage leaves, the greatest number and the largest of them are found on the lowermost part of the shoot where the internodes are shorter, partly in the soil, and partly immediately above its surface; they gradually decrease in size upwards; thus we have, besides the foliage leaves on the elongated portion of the aerial stem, also a more or less marked radical rosette; I therefore call these partial rosette plants (Fig. 25).

Finally we have the genuine rosette plants in which all or nearly all of the foliage leaves are situated in a radical rosette, and the elongated aerial shoots produce flowers only.

20. **Proto-Hemicryptophytes** are Hemicryptophytes whose leaf- and flower-bearing aerial shoots are elongated from the base. The largest foliage leaves are as a rule borne by the middle portion of the stem or thereabouts, and from this point they decrease in size towards the base and towards the apex of the shoot. The leaves situated immediately above the soil are more or less scale-like and serve to cover the buds during the unfavourable season. The shoots are thus essentially like those of Phanerophytes, and this resemblance is even more marked if we look at seedlings and at shoots not about to flower. Even in the year in which they germinate Proto-Hemicryptophytes develop an elongated aerial shoot entirely resembling those of the Phanerophyte and unlike that of the other Hemicryptophytes. Even later in the plant-life we usually see that even the shoot which is not destined to flower develops into an elongated aerial shoot (Fig. 21, A). By this behaviour Proto-Hemicryptophytes demonstrate their position as representing the first stage in adaptation to life in the soil.

Just as within the Chamaephytes, Suffruticose Chamaephytes often pass imperceptibly into Herbaceous Phanerophytes and Nanopherophytes, so the Proto-Hemicryptophytes pass imperceptibly into the Suffruticose Chamaephytes (Fig. 22), from which most of them are certainly descended. The type is distributed both in warm parts of the world with an unfavourable season, a dry period, and also in the colder regions of the world, where the unfavourable season is a cold winter. In the latter regions tuberous structures for food storage appear to be rare (Fig. 23); in the former regions on the other hand we often see large tuberous parts of the stem situated in the soil; these organs presumably function as water storers in the dry season. Vegetative distribution over wide areas is not common, since most, at any rate of the European species, are without stolons.

A. WITHOUT STOLONS. In some the primary root persists, in others, doubtless the majority, it ultimately dies, and the older portions of the subterranean stem system gradually die too, so that reproduction by division takes place, when the connexion between the different shoot systems is severed. But since these plants have no stolons they cannot multiply copiously in a vegetative manner; their growth is usually more or less densely tufted. Examples are: *Thalictrum flavum, T. flexuosum, T. minus, Hypericum hirsutum, H. pulchrum, H. montanum, H. perforatum, H. quadrangulum, H. tetrapterum, Euphorbia salicifolia, E. dulcis, E. virgata, &c., Veronica longifolia, V. latifolia, V. sibirica, V. teucrium, V. austriaca, Verbena officinalis, V. littoralis, V. bonariensis, V. urticifolia, Linaria genistifolia, L. purpurea, L. italica, L. dalmatica, Scrophularia laterifora,*
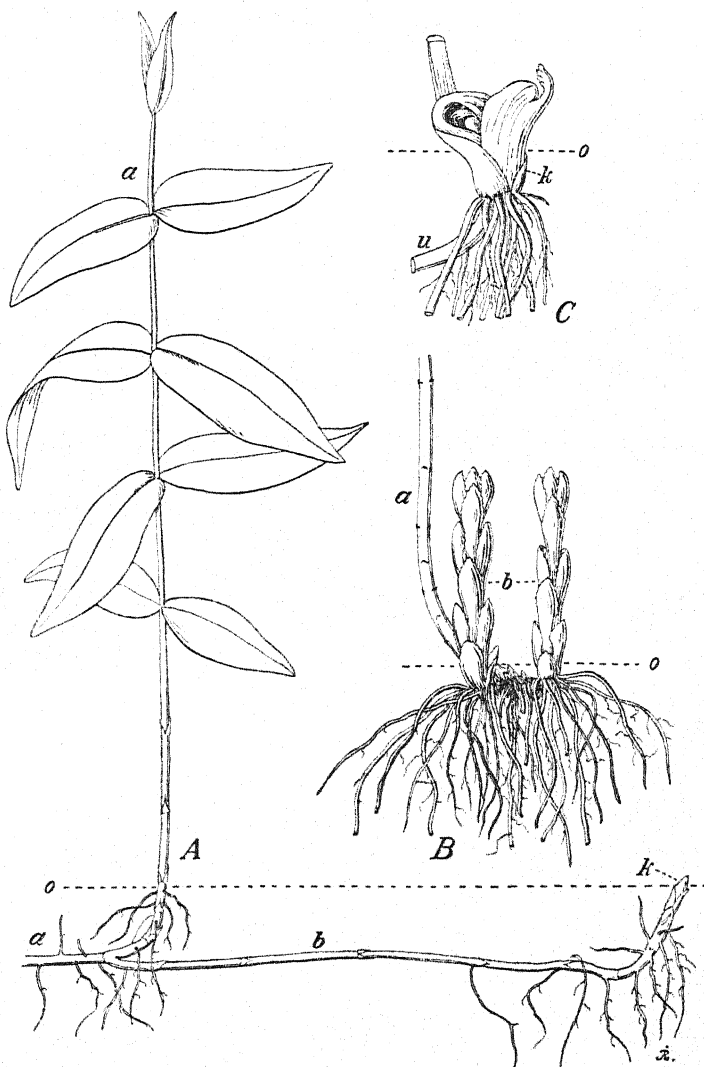
Fig. 21. A, *Lysimachia vulgaris*; a proto-hemicryptophyte; the shoot *a*, although not destined to flower, has developed an elongated aerial portion, which will die at the close of the growing period; from the underground portion of this shoot there springs a new subterranean lateral stolon, *b*, which bends up at its apex so that the winter bud, *k*, is situated in the soil, *o*. (¼). B, *Epilobium montanum* in its spring condition; *a*, last year's dead shoot; the winter buds, *b*, which are now expanding, were situated in the soil, *o*. (½). C, *Aegopodium podagraria* in spring; *u*, the apex of a stolon with the bud, *k*, which is situated in the soil, *o*, and is now expanding. (¼)

S. *nodosa*, S. *vernalis*, S. *canina*, S. *alata*, *Astragalus glycyphyllus*, *Ono-brychis viciaefolia*, *Melilotus albus*, M. *altissimus*, M. *officinalis*, *Medicago*

FIG. 22. *Nepeta latifolia*: shoot system in the autumn stage; *a*, persistent portion of a shoot that flowered in 1903. *b*, lowermost persisting portion of shoot that flowered in 1904; the buds attached to this are in the soil; they will develop next year, and have already in the autumn of 1904 grown out into leafy shoots, *c*, with a short lateral shoot, *d*, situated in the soil-surface. Under favourable conditions the aerial portion of the shoot, *c*, may survive the winter, and the plant can thus grow as a Suffruticose Chamaephyte. ($\frac{2}{3}$)

falcata, M. *sativa*, *Epilobium roseum*, E. *montanum*, *Ballota nigra*, *Lamium album*, *Marrubium vulgare*, *Nepeta cataria*, N. *latifolia* and many other Labiates; further *Cynanchum vincetoxicum*, many species of *Galium*, many

Composites: species of *Artemisia, Inula, Aster, Hieracium, Solidago,* and many other genera.

B. WITH STOLONS. Some species may have both subterranean and epigeal stolons, e.g. *Stachys silvatica* and other Labiates; further *Urtica dioica*. Examples of plants with subterranean stolons are *Epilobium tetragonum, E. obscurum, E. palustre, E. parviflorum, E. hirsutum, Lysimachia vulgaris* (Fig. 21, A), *Mercurialis perennis, Saponaria officinalis,* various *Labiatae* and *Leguminosae* (for example species of *Lathyrus* and *Orobus*).
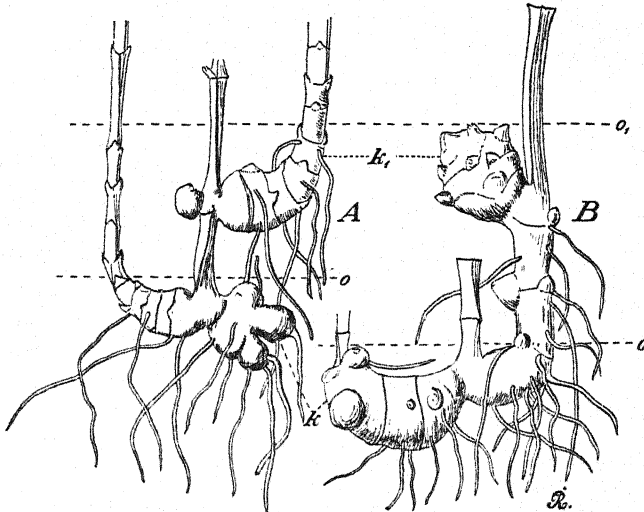
FIG. 23. *Scrophularia nodosa*; two plants, which have become covered with a layer of soil, $o-o_1$; the new tubers, k_1, with the winter buds, are not formed like the others immediately beside the old tubers, k, but higher up, i.e. in the soil-surface. ($\frac{3}{4}$.)

Among Proto-Hemicryptophytes must also be reckoned our species of *Rubus*, of which, however, most occupy a peculiar position within this sub-type. Our species of the sub-genus *Cylactis*, namely *Rubus chamaemorus* and *R. saxatilis*, are genuine Proto-Hemicryptophytes, the former without and the latter with stolons. All our other species, namely species of the sub-genera *Idaeobatus* and *Eubatus*, deviate in that the aerial shoots do not die at the end of the growing period, but surviving the unfavourable season, live for one more growing period, and then die; they thus have a biennial aerial life; the first year they are vegetative, bearing only leaves, in the second year they produce the flowering lateral shoots, and then die down to the subterranean portion, from which the shoots arise that are to carry on the next year's growth. Although the aerial shoots thus live for two years it is only the buds on the flowering shoots which survive the unfavourable season on shoots which project into the air, while the vegetative buds, on which the continuation of the

individual life depends, are always found on the part of the shoot situated in the soil-surface (Fig. 24), as in the other Proto-Hemicryptophytes. I therefore consider that these species of *Rubus* belong to that group. It is not necessary for the continuance of the individual that the aerial shoot should survive the unfavourable season. In some species the vegetative shoots are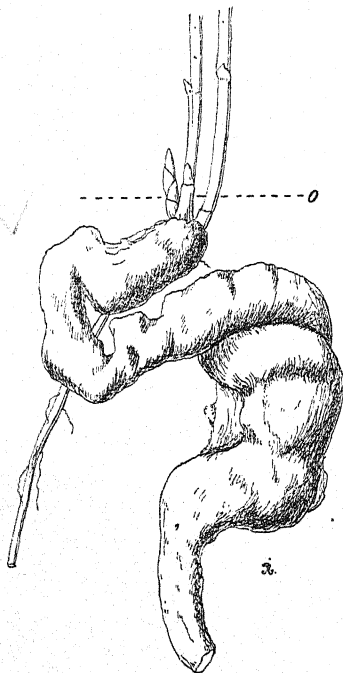 erect or arched, but throughout their whole length they are free aerial shoots. These species belong to the Proto-Hemicryptophytes without stolons: examples are *Rubus idaeus, R. suberectus,* and *R. plicatus.* In most of the species they are so strongly arched that their apices with the terminal buds reach the ground, where they root and are gradually covered by 'hilling'. The next year the terminal bud grows out to form a vegetative aerial shoot, which, when the old stem dies, becomes quite free from the mother plant, so that vegetative re-production, and distribution take place. The distribution can go on very actively, the stem sometimes attaining as much as 7 metres in length. These species belong to the Proto-Hemicryptophytes with stolons. Each runner grows from its terminal bud into a new runner the following year, and in this way there ultimately arises a monopodium which forms an undulating line; the crests of the waves in this line are formed of the arched aerial portions of the shoot, and the troughs are formed of the shoot-apices

FIG. 24. *Rubus* sp. in spring. *o*, soil-surface. ($\frac{1}{3}$)

which are carried down into the soil-surface so that the terminal bud may be protected during the unfavourable season. In this way new seats are formed for the origin of several monopodia, for besides the terminal bud which continues the monopodium already laid down, there are also a varying number of lateral buds from which the beginnings of new monopodia arise.

21. **Partial Rosette Plants.** In these plants too the aerial shoot bears foliage leaves as well as flowers, but the largest leaves and also often the greatest number of them are attached to the lower portion of the shoot, where the internodes are more or less contracted, so that they form a kind of rosette (Fig. 25). The shoot is usually biennial; in the first year the radical rosette is formed, in the second year an elongated aerial shoot with foliage leaves and flowers.

As in the Proto-Hemicryptophytes the aerial portion of the shoot bears foliage leaves, but in the partial rosette plant the greatest development of leaves extends from the middle of the stem to its contracted
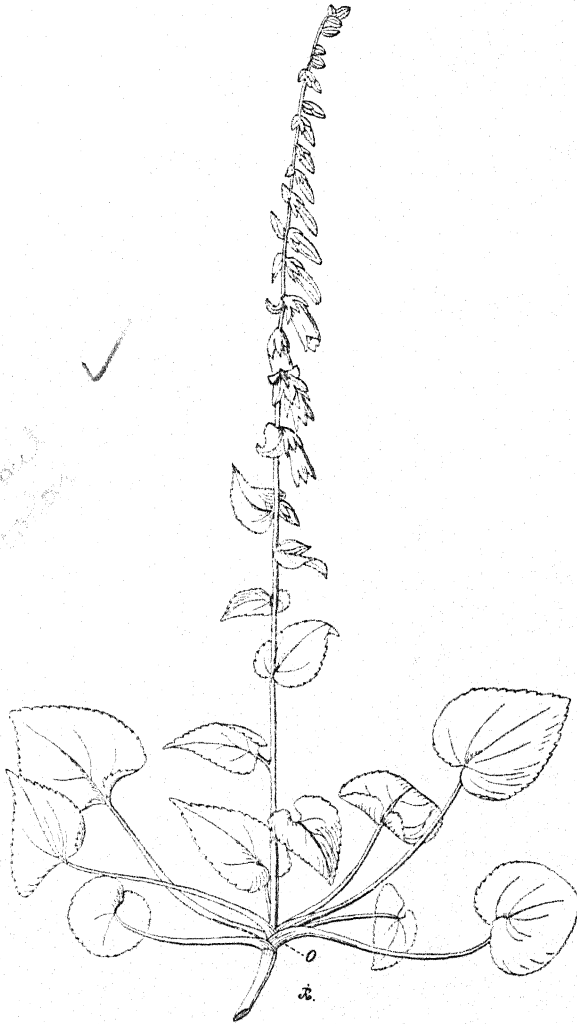

FIG. 25. *Campanula lamiifolia*; partial rosette plant. *o*, soil-surface. (¼)

lowest portion, so that a transition is formed from the rosette plants in which the elongated aerial portion of the shoot bears only flowers and the foliage leaves are all gathered into a rosette at the base. Most of these plants are without stolons. They live principally in temperate regions where the summer is not too dry, and where the ground is covered with snow for a longer or shorter period; Central Europe is the centre of

their distribution. Besides a great number of perennial herbs the bulk of biennials belong here too.

A. WITHOUT STOLONS. Many species of the following families: *Caryophyllaceae*, e.g. *Viscaria viscosa, Melandrium rubrum* and *M. album, Lychnis flos cuculi*, species of *Silene, Dianthus*; *Ranunculaceae*, e.g. *Caltha palustris, Ficaria ranunculoides, Ranunculus flammula, R. auricomus, R. acer, R. lanuginosus, R. polyanthemus,* and other species, *Helleborus, Aquilegia, Aconitum, Delphinium,* and many others; *Rosaceae*, e.g. *Agrimonia, Poterium, Sanguisorba,* and *Spiraea*; *Umbelliferae*, e.g. *Anthriscus silvester, Oenanthe Lachenalii, Cnidium venosum, Libanotis montana, Angelica silvestris, Selinum carvifolium, Peucedanum oreoselinum* and *P. palustre, Laserpitium latifolium* and many others; *Campanulaceae*: many species of *Campanula,* and *Phyteuma*; *Dipsaceae*: species of *Dipsacus, Knautia, Scabiosa,* and *Succisa*; *Compositae,* e.g. species of *Lappa, Serratula, Carduus, Cirsium, Centaurea, Arnica montana, Solidago virga aurea, Erigeron acer, Aster tripolium, Aracium paludosum, Picris hieracioides, Lactuca muralis, L. scariola, Chrysanthemum leucanthemum, Cineraria campestris, Senecio erucaefolius, S. jacobaea, S. aquatica* and others, *Inula helenium, I. vulgaris, Hieracium vulgatum, H. murorum, H. caesium* and many others; *Grasses,* most of our tufted species, e.g. *Aira caespitosa, Dactylis glomerata,* species of *Schedonorus, Festuca, Poa, Cynosurus,* &c. Species of *Rumex,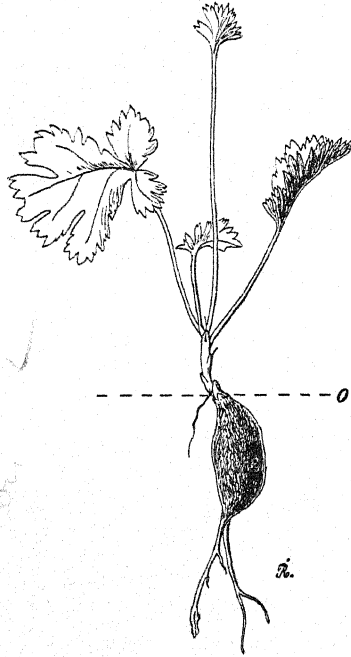 Chelidonium majus, Glaucium flavum, Nasturtium anceps, Cardamine pratensis, C. amara, Barbarea lyrata, Alliaria officinalis, Malva alcea, M. moschata, M. silvestris, Saxifraga granulata, Anthyllis vulneraria, Samolus Valerandi, Myosotis, Verbascum, Digitalis, Veronica, Pedicularis, Betonica, Brunella, Ajuga,* &c., &c.

FIG. 26. *Pelargonium flavum.* Hemicryptophyte with hypocotyl (?) stem tuber; a young plant. *o,* surface of soil. (½)

B. WITH STOLONS. The following have aerial stolons: *Ajuga reptans* and *Ranunculus repens.* The following have subterranean stolons: *Aegopodium podagraria, Cirsium heterophyllum, Tanacetum vulgare, Achillea millefolium,* and a number of grasses and sedges.

22. Rosette Plants. The aerial elongated portion of the shoot in these plants is almost exclusively flower-bearing, while the foliage leaves are attached close together to that portion of the shoot which is situated in

the soil-surface (Fig. 27). This life-form is the one that has undergone most transformation for adaptation to life in the soil-surface; during the whole of the vegetative period the shoots remain in the soil-surface; only when the plant flowers is there formed an aerial shoot, or scape.

In most of them the underground stem is a sympodium, and the development of the shoot is biennial (not counting the bud stage); in the first year a rosette of leaves is formed and the second year a flowering aerial portion, which ends the life of the shoot.

For efficient carbon assimilation it is very important that the closely packed leaves of the rosette should not shade one another more than is
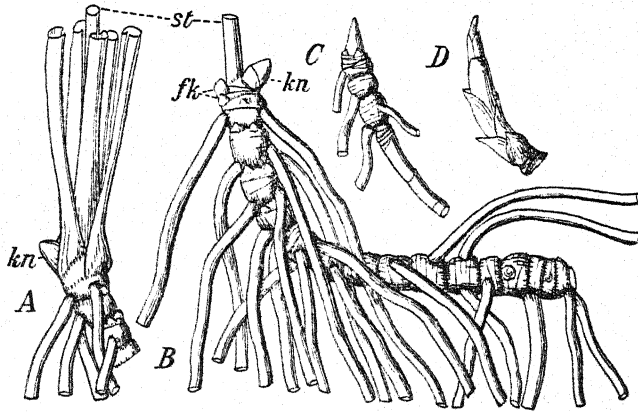

Fig. 27. Rhizomes of *Anthericus ramosus*; a Hemicryptophyte (Rosette plant). The winter buds— *kn* in A; *fk* and *kn* in B, C, and D—are situated in the soil-surface; *st*, the lowest portion of the flowering stem with the radical rosette. (c. ⅓)

absolutely necessary. This end is reached by various devices; sometimes the leaves are borne on long stalks, so that the blades are separated (examples *Drosera*, *Viola*, *Petasites*); sometimes the same result is attained by the leaves being long and narrow (examples *Luzula*, Grasses and Sedges). But the most characteristic rosette leaf has a narrow base from which it gradually broadens towards the apex, in other words it gradually broadens as the space at its disposal increases. Leaves of this kind may be obovate, spathulate, or of other forms; examples include the most characteristic rosette plants, *Sempervivum*, *Primula*, *Plantago*, *Bellis* (Fig. 28), *Hieracium pilosella*, *H. auricula*, *Taraxacum*, *Hypochaeris maculata*, and many others. But even if the form of the leaf be the one best suited for its own illumination, that would not suffice if the arrangement and direction of the leaves were not such as to prevent them standing immediately above one another. Thus the leaves of rosette plants are not merely as a rule alternate, but there are a great many leaves in each spiral, so that many leaves are developed before one arrives at a point immediately above an already developed leaf. Even

when this occurs, it does not follow that the last developed leaf shades the leaf below, for it often happens that a leaf does not project in the same direction as the one immediately below it, but deviates slightly to one side, thus scarcely obscuring the lower leaf. We must consider too that the youngest leaves are still small and cover only the narrow basal portion of the older leaves, so that all the space is used in the best possible way (Fig. 28). We see in su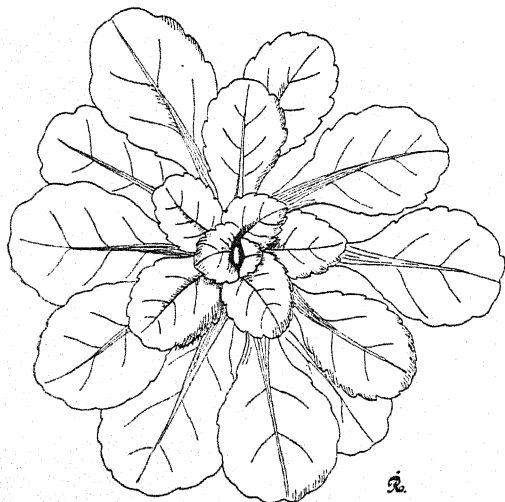ch rosettes a greater number of rows than the phyllotaxy would lead us to suppose possible: an especially good example of this is *Crassula orbicularis* (Fig. 29), which has a marked rosette with opposite decussate leaves. The leaf arrangement can be easily seen from the young leaves in the middle of the rosette. The leaves do not stand out, as one would expect, in four directions, but because of the process of twisting, which begins early, they come to stand out in a great many directions, just as if the plants had spirally arranged leaves, numerous in each turn of the spiral.

FIG. 28. Rosette of *Bellis perennis* seen from above. ($\frac{1}{1}$)

Rosette plants belong principally to regions where the ground is covered with snow in winter. Most of them have winter-green leaves, which are protected by the snow; they can begin assimilation immediately at the beginning of the favourable season.

A. WITHOUT STOLONS. Examples of Danish plants: *Drosera, Statice, Limonium, Primula, Bellis, Taraxacum, Thrincia, Leontodon, Hypochoeris, Triglochin maritimum, Liparis Loeselii* (Fig. 31), *Malaxis paludosa, Spiranthes spiralis* (Fig. 32, B), some species of *Luzula*, Grasses and Sedges, especially species of *Carex*.

B. WITH STOLONS. *Petasites, Hieracium pilosella, H. auricula*, &c., *Triglochin palustre, Scheuchzeria palustris, Goodyera repens* (Fig. 32, A); and some Grasses and Sedges. In some the stolons are epigeal, for example *Hieracium* sp., but in most they are subterranean.

MONOPODIAL ROSETTE PLANTS. In the examples of Rosette plants mentioned above, the subterranean stem system is a sympodium, but I include among Rosette plants also Hemicryptophytes whose rhizomes are monopodia. Some of the species belonging here are marked Rosette plants; but others on close examination are found to resemble partial

Rosette plants, or even Proto-Hemicryptophytes, since the aerial shoots bear foliage leaves. If I include them among Rosette plants it is because the aerial shoots have no direct significance for the plants' ability to survive the unfavourable seasons. The aerial shoots die back to the base, so that their lowermost parts situated in the soil-surface do not bear buds destined to survive the unfavourable period of the year; the surviving buds are found exclusively on the monopodium, which is situated in the

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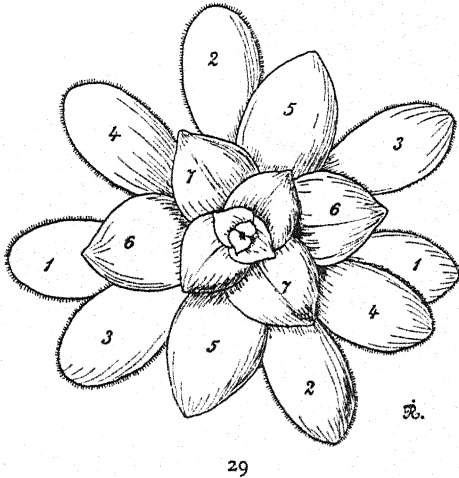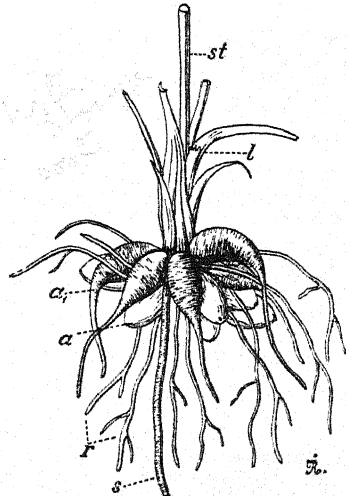
FIG. 29. *Crassula orbicularis*; a leaf rosette formed of opposite decussate leaves, which during development twist so as to produce a many-rayed rosette; the leaves belonging to the same pair are marked with the same number.

FIG. 30. *Ranunculus millefolius*. Hemicryptophyte (Rosette plant), with storage roots, a; l, the sheaths of the radical leaves; st, the lowest portion of the flowering stem. (†)

soil-surface itself, usually has short internodes, and never grows out to form an aerial shoot. Moreover this type of plant appears to be best adapted for life in the soil-surface, showing as it does, the most thorough division of labour for the tasks imposed upon the plant in adapting itself to favourable and unfavourable periods. By grouping both types together it is possible to give a complete picture of their interesting behaviour. In the following short conspectus the most primitive types are put at the beginning.

A. The monopodial axis bears only foliage leaves, and no scales. In the axils of these leaves arise partly new contracted monopodial axes, which are situated in the soil-surface, partly aerial shoots which either bear both flowers and foliage leaves, or flowers alone; in the latter case the species may or may not have stolons.

a. The aerial shoots bear foliage leaves; proper stolons usually absent. Examples of Danish plants: *Viola silvatica, V. mirabilis, Geum, Alchemilla vulgaris* and allied species, *Potentilla incana, P. verna, P. opaca, P. silvestris, Trifolium pratense.* *Carex strigosa* also most nearly approximates to this division.

b. The aerial shoots without foliage leaves, bearing only flowers.

o. Without stolons.

Examples: *Viola hirta, Plantago major, P. media, P. lanceolata,* and *P. maritima, Pinguicula vulgaris* and *Carex digitata.*

oo. With stolons.

Examples: *Viola odorata, Fragaria, Potentilla sterilis, P. reptans, P. procumbens, P. anserina, Trifolium repens, T. fragiferum,* and *Sagina procumbens.*
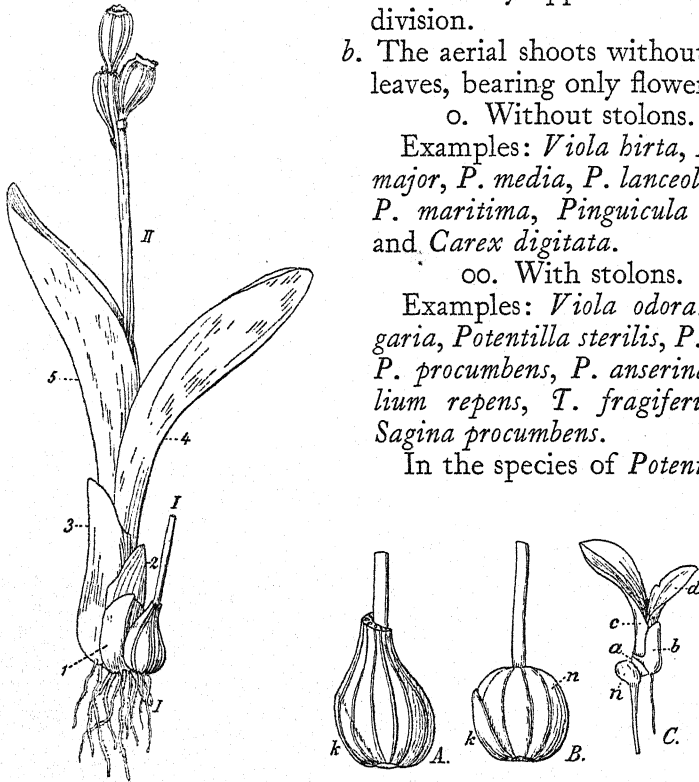
In the species of *Potentilla* it is

FIG. 31. *Liparis Loeselii;* Hemicryptophyte (Rosette plant) with stem tubers formed of the lowermost portion of the flowering stem enclosed by leaf-bases; the winter bud is situated at the base of the tuber in the soil-surface; it arises in the axil of the uppermost leaf, 5; I, last year's tuber with the lower portion of last year's flower-stem. (†)

A, the lowest tuberous portion of the flowering stem surrounded by the sheath of the uppermost leaf; the presence of the bud, *k,* can be made out within the sheath; in B all the leaves have been removed and the bud, *k,* is seen more clearly. C, young plant with no flowering axis; *n,* the old tuber; *a–d,* the new shoot's four leaves which surround the new tuber. (*c.* ⅔)

the flower-bearing stem that forms the runners, its reaction to gravity being changed so that instead of being negatively geotropic it grows at right angles to the direction of gravity, thus lying along the earth, to which it soon becomes rooted; it is only the flowering stalks that are negatively geotropic.

B. The monopodial axis bears both scales and foliage leaves; in each period of growth there are developed a series of each kind; after the

foliage leaves have unfolded at the beginning of the period of growth there are formed a series of scales for the protection of the young foliage leaves and flowers, which unfold the following year.

a. Without stolons.

Example: *Anemone hepatica*; with solitary flowers in the axils of scales; the foliage leaves remain green through the winter.
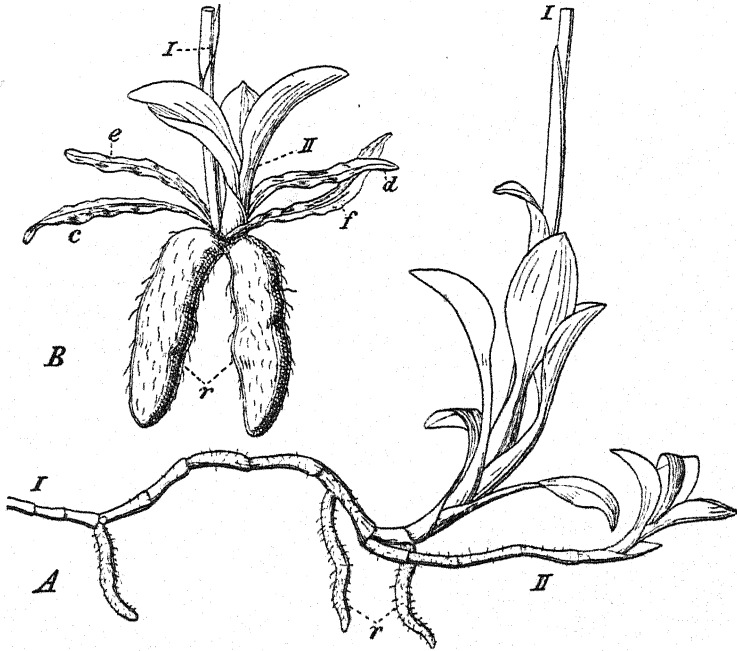

FIG. 32. A, *Goodyera repens*; Hemicryptophyte (Rosette plant) with Stolons; I–I, Flowering shoot; II, a lateral axis arisen from I, with a winter rosette. (†). B, *Spiranthes spiralis*; Hemicryptophyte (Rosette plant) with storage roots, *r*; I, the flower-shoot whose leaves, *c–f*, are now withered; II, lateral shoot destined to spend the winter in the soil-surface. (†)

b. With stolons.

Convallaria majalis; the vertical rhizome usually produces only two foliage leaves during each period of growth, and after that three to seven scales which surround and protect the foliage leaves and flowers of the coming year. The flowers arise in the axils of the uppermost scale. The stolons, which are subterranean and sometimes branched, arise in the axils of foliage leaves. After a longer or shorter period of growth the tips of the stolons bend up into the soil-surface, where they grow into a monopodial axis like the mother shoot.

Oxalis acetosella (Fig. 33) is best included here. It certainly does not possess a vertical rhizome with runners like the plants just mentioned, but the monopodium, itself horizontal, resembles a stolon, bearing thick scales (Fig. 33, A, *n*) and foliage leaves, whose

swollen basal portion (Fig. 33, A, *b*) remains attached after the petiole and leaf are dead, and, like scale-leaves, serves for storing nourishment. The flowers are attached singly in the leaf axils. The rhizome of this plant is indeed situated in the soil-surface, but it is

FIG. 33. *Oxalis acetosella*. A, plant with elongated rhizome creeping horizontally under and amongst fallen leaves; the single shoots are monopodial axes with flowers arising laterally in the leaf axils; *l*, the lowest portion of two leaf stalks, *n*, scale leaf; *b*, persistent fleshy basal portion of a fallen leaf; in the axil of one of these is seen a fruiting stem. B, a contracted shoot in the soil-surface on somewhat firm ground not covered with leaves; it bears a great number of closely packed scale leaves and a very great number of leaf bases of fallen leaves, *r*. ($\frac{2}{3}$)

covered by a layer of leaves thus forming a transition to the Crypto-phytes; but as it can also live where there is no leaf covering, when the rhizomes remain in the soil-surface, the plant may be reckoned among the Hemicryptophytes.

C. The monopodial axis bears only scale-leaves; the aerial shoots there-fore always bear foliage leaves as well as flowers. Of Danish plants the only representative is *Gentiana pneumonanthe*; *Sedum rhodiola* is an exotic example.

A GENERAL VIEW OF THE HEMICRYPTOPHYTES. Now that the most important types of Hemicryptophytes have been mentioned, let us take a general view of these plants collectively in order to see in what manner and in what degree they have become modified in comparison with the Phanerophytes, from which they are certainly derived. We must consider here not only those changes of external form, but also the alterations in the internal economy of the plants which are connected with their capacity to react in a definite manner to the stimuli of gravity and light, the reactions which are of special importance in determining the direction of growth.

In Proto-Hemicryptophytes there is, apart from the stolons possessed by some species, usually no alteration in the reaction of the shoots to gravity and light; the shoots are constructed like those of Phanerophytes, and they share their negatively geotropic growth. These plants have become Hemicryptophytes only because the shoots, by reason of the unfavourable climate, die back to that portion of the stem which is situated in the soil-surface, and which alone bears winter buds. The close relationship between Proto-Hemicryptophytes and Phanerophytes is seen from the fact that they form an aerial shoot in the year in which they germinate, even if the shoot is not destined to bear flowers. And, even if the individual has become capable of flowering, it forms shoots that are purely vegetative, besides the flowering shoots. In this connexion it is worth noting that when flowering ceases there is often a copious development of purely vegetative lateral shoots even from the uppermost flower-bearing parts of the plants. All these shoots die just as the mother shoot does at the advent of the unfavourable season. But these plants (e.g. *Urtica dioeca*) give the impression that, if the external conditions remained favourable during the whole year, they would behave like Phanerophytes, and it is therefore not surprising that certain plants (e.g. some *Labiatae*), which in the Mediterranean region are small shrubs, grow with us as Proto-Hemicryptophytes.

Looking next at the other kinds of Hemicryptophytes we observe that there has occurred in the more pronounced partial Rosette plants and in the real Rosette plants an alteration in their reaction; the shoots during their first purely vegetative stage of development react to light by almost entire suspension of growth in length, while a copious development of foliage leaves is taking place, thus bringing about the development of a rosette. Not till the shoot is about to flower does its reaction alter, so that a marked elongation occurs. In the few plants which have an upright monopodial axis, whose apex never develops an inflorescence, the shoot has to remain at the first stage, in which growth in length does not occur.

That the shoots in partial rosette plants and rosette plants do not grow in length when they reach the soil-surface is not due only to internal causes, but is determined by light. This is seen from the fact that the

shoots which begin growing at some depth in the soil develop elongated
internodes as long as they remain in the soil, but become contracted as
soon as they reach the surface. If such plants are covered with a layer of
earth of varying thickness they develop elongated shoots until they again
reach the surface; examples: *Campanula trachelium* (Fig. 34), *Ranunculus
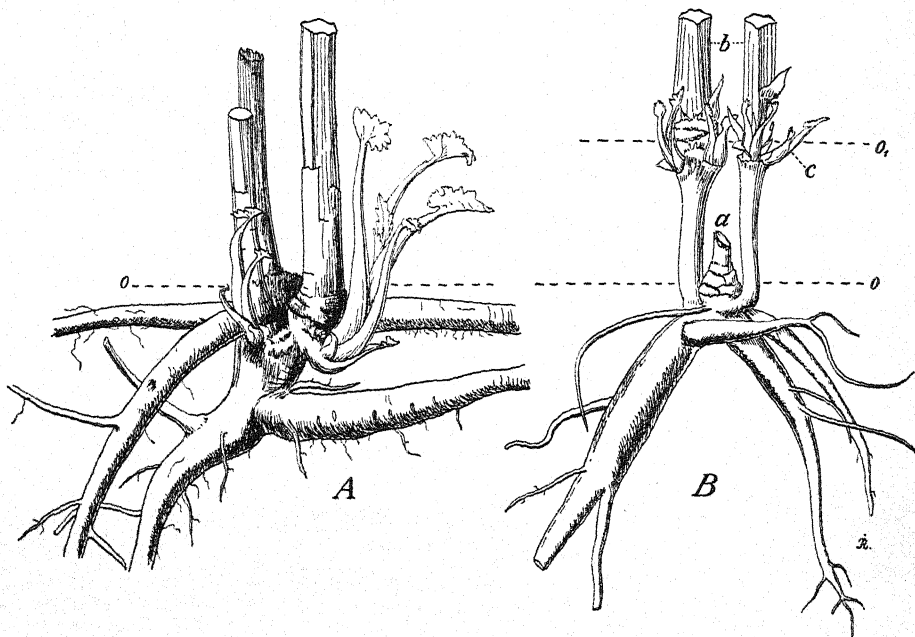bulbosus* (Fig. 35), *Taraxacum vulgare* (Fig. 36) and *Bellis*. The rosettes

FIG. 34. *Campanula trachelium* in spring; partial rosette Hemicryptophyte. A, the plant under
ordinary circumstances; *o*, the soil-surface. B, a plant which has become covered with a layer of soil,
o–*o*$_1$; the shoot, *b*, which has developed after this covering has been laid down, has made an elongated
stem in its portion covered with earth; only after reaching the light above the new soil-surface, *o*$_1$, has
it formed a rosette of foliage leaves, in whose axils, *c*, the winter buds are laid down. ($\frac{2}{3}$)

are in this way insured both against rising too high above the ground
and against being buried, and this distinguishes these plants as marked
Hemicryptophytes. Both Rosette plants and partial Rosette plants are,
already in the first stage of their life, i.e. in the year in which they
germinate, differentiated from Proto-Hemicryptophytes by producing
during that year only rosettes and not elongated aerial shoots, which
are not developed until the plants are about to flower. The primary
shoots of Proto-Hemicryptophytes, as already mentioned, grow out in the
year of germination to form elongated aerial shoots.

We have already seen how the rhizomes of Hemicryptophytes, because
of their annual growth, however small this may be, rise higher and
higher up, and how they are prevented from rising too high above the

earth, partly by the deposition of dry plant remains, partly by 'hilling', especially through the activity of worms, and partly because the rhizomes of many are dragged down by the contraction of the roots.

Lastly let us briefly consider the fact that many Hemicryptophytes possess shoots which, at any rate during the first stage of their life, react to gravity differently from the ordinary aerial shoots. I refer to the so-called 'stolons' which serve for vegetative distribution and multiplication.
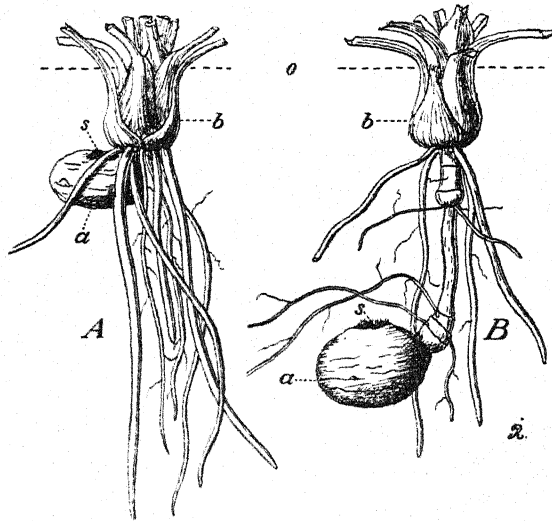

FIG. 35. *Ranunculus bulbosus*; Hemicryptophyte (Rosette plant) with tuberous underground stem. *a*, last year's tuber; *s*, scar of last year's flowering stem; the sheaths of the radical foliage leaves, *b*, are situated on and surround the new tuber. During the development of this tuber and the leaves and inflorescence connected with it, the stored-up material in the old tuber, *a*, is consumed. *o*, the present soil-surface; in B, the last year's soil-surface was a little above *s*; after that the plant was covered with earth, so that the soil-surface was raised to *o*; the new plant, which is a lateral shoot of the old tuber, has not formed the new tuber and leaf rosette, as it otherwise would, beside the old tuber, but it has first formed an elongated slender shoot, and when this has reached the soil-surface a new tuber and leaf rosette were formed.

They are, at any rate to begin with, horizontal or nearly so, but sooner or later they bend upwards to form an upright portion which strikes root and becomes a separate individual when the horizontal portion of the stolon dies. Only very rarely are the vegetative shoots of plants constantly horizontal; e.g. *Oxalis acetosella*. We often find in the axils of the leaves of the stolons buds which are also capable of forming new individuals, either by immediately making an upright shoot which becomes rooted, or by growing out into horizontal stolons, which ultimately bend their tips upwards and become rooted at the base. The buds and shoot-apices of these stolons, which are destined to survive the unfavourable period, are lodged in the soil-surface as are the buds of the ordinary shoots. This further serves to characterize these plants as marked Hemicryptophytes.
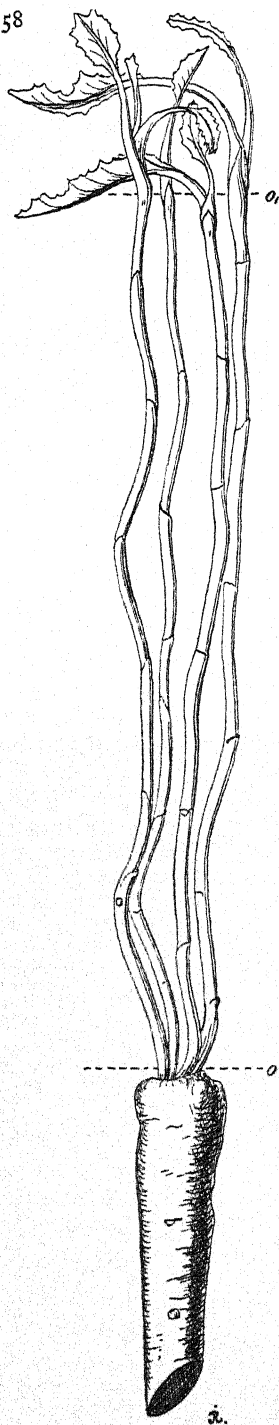
In some species the stolons are always epigeal (*Fragaria, Potentilla anserina, P. reptans,* and other species, *Hieracium pilosella,* and many others). In other plants they are always subterranean (*Petasites,* some Grasses and Sedges, &c.). As mentioned before there are some plants which have both epigeal and subterranean stolons (*Urtica dioeca, Stachys silvaticus,* species of *Mentha,* &c.). It sometimes happens in these plants that the same stolon during part of its course is epigeal and in part of its course subterranean or at least covered by fallen leaves (Fig. 37).

Neither the subterranean nor the epigeal stolons have been thoroughly investigated; but as far as inquiries go the epigeal stolons seem to behave like the horizontal shoots of the active Chamaephytes already described, growing in light at right angles to gravity and being negatively geotropic in the dark. Czapek and more especially Maige have shown this to take place in the following species: *Rubus caesius, Potentilla anserina, Ranunculus repens, Trifolium repens, Mentha aquatica, Stachys silvaticus, Ajuga reptans, Hieracium pilosella.* I found the same behaviour in my experiments with *Veronica serpyllifolia* and *Brunella vulgaris.* When I grew the stolons of these plants in the dark, keeping them in a case impervious to light, but not otherwise interfering with them, the apex of the stolons grew upwards. When on the other hand the stolons were held in a vertical position with their apices upwards and in light, they continued their growth horizontally or obliquely downwards. Growth obliquely downwards in my experiments was marked in *Hieracium pilosella,* whose shoots by this growth became tightly pressed to the soil.

Among the plants whose runners grow

FIG. 36. *Taraxacum vulgare;* a Rosette plant which after being covered with earth is bringing its bud up to the soil-surface by the elongation of the shoots; not till the apices have reached the light are there developed short internodes with leaves and rosette. *o,* the original soil-surface; o_1, the later soil-surface. (⅓)

horizontally in light, but are negatively geotropic in the dark, Maige mentions *Nepeta glechoma* and *Potentilla reptans*. According to Czapek on the contrary these two species grow horizontally both in light and in darkness; that investigator finds that the shoots of *Linaria cymbalaria* behave in the same way. I found this kind of horizontal growth both in light and darkness in *Ajuga reptans* (a variety with reddish-brown leaves) and *Ranunculus repens*, thus deviating from the results of Maige. In some species the stolons are negatively heliotropic (*Nepeta glechoma* according to Wiesner and Maige, and *Potentilla reptans* according to Maige). In other species they are slightly positively heliotropic (*Hieracium pilosella* and *Mentha aquatica* according to Maige). The heliotropism
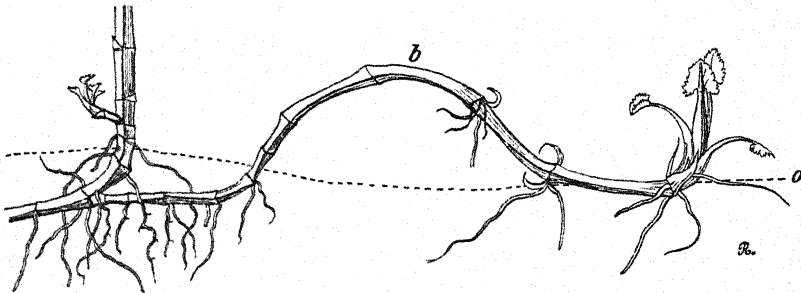
FIG. 37. *Stachys silvaticus*; the lowermost portion of a flowering shoot with a stolon whose apex has arisen above the soil-surface, *o*; it is then bent downwards, and on again reaching the soil-surface it is rooted and begun to form foliage leaves.

varies no doubt with the light's intensity, and this behaviour may explain why Wiesner and H. de Vries find the stolons of *Fragaria* negatively heliotropic, and Czapek describes them as positively heliotropic.

As already mentioned both subterranean and epigeal stolons may be found in *Stachys silvaticus* and *Urtica dioeca*; doubtless as a rule the stolons are situated actually in the soil-surface; the subterranean stolons most usually lie near the surface, so near the surface perhaps that sufficient light can reach them to counteract their geotropism and make them grow at right angles to the direction of gravity; otherwise it is difficult to understand why the subterranean stolons should grow horizontally, for in the absolute darkness of a case impervious to light the stolons of these plants grew erect, and were thus negatively geotropic. Moreover I planted some individuals of the above named species in the soil-surface and some at a depth of 15 cm.: in the former the new stolons lay above the soil or actually in the soil-surface partially exposed to light; in the latter some stolons came off at a considerable depth, but they grew at once almost vertically up through the soil until they reached the surface, when they grew horizontally. Even if it seems to be general for the epigeal stolons of Hemicryptophytes to be negatively geotropic in the dark, and, because of an altered reaction towards gravity, vertical in the light, yet all of them

do not behave in this way. The slender stolons of the well-known *Saxifraga sarmentosa* appear to be entirely insensitive to gravity, at any rate in the dark. A number of stolons, connected all the time of course with the mother plant, were brought into the dark and so fixed that some were horizontal, others vertical with their apex upwards, others again vertical with their apex downwards. They all went on growing in the direction in which they had been fixed. On the other hand they were very sensitive to light, being negatively heliotropic in moderately strong light. When lighted from one side in a greenhouse which had windows only on its southern side, four stolons, which were fastened with their apices erect, first curved over in a horizontal direction, and then arched downwards, always away from the light, even if by so growing they came to have the side which had been formerly turned upwards directed downwards.

Although much remains to be investigated about the causes determining the direction of the stolons in Hemicryptophytes, we do at least know something about these causes, and we know the methods to employ in order to learn still more. On the other hand we are entirely in the dark about how stolons arose, about what determined negatively geotropic shoots to alter their reaction towards gravity and grow at right angles to its attraction. We encounter here, as at so many other points, the question of the origin of species, or what comes to the same thing, the formation of new hereditary characters.

Let us here discuss some circumstances and some recent investigations which may possibly have significance for the solution of the problem of the origin of stolons.

There are species of plants in whose flowering shoots we see imperceptible gradations between lateral flowering shoots and stolons. For example in *Stachys silvaticus* we can trace lateral branches from the top of an erect mother shoot to the portion situated in the soil-surface. The uppermost of these branches are comparatively short, erecto-patent, and bear flowers; but the farther we go down the stem the longer they become, and their proximal vegetative portion becomes longer and spreads at a wider angle. Right down on the soil, but still wholly in the light, we find long branches which either project into the air or rest on the ground, and bear only a few flowers at their apex, or are quite flowerless. If they are flowerless they can root and live through the winter: they have in fact become stolons, which, in this species either lie in the soil-surface, or partially or entirely above the ground. The stolons of this species are, like those of all plants furnished with a sympodium and stolons, lateral shoots which do not flower the same year as the mother shoot, but delay their flowering until the following year. Stolons thus differ from the branches which arise higher up on the mother shoot. In the first growth period they grow horizontally along the earth or buried

in it, thus obtaining protection from the effects of the unfavourable season. It is by this means, in fact, that they are enabled to survive the winter. Not till the next growth period do they turn upwards to form a vertical flowering shoot. Thus we see in all sympodial plants with stolons that it is only in the first period of development that the stolons grow at right angles to the pull of gravity; at another period, during the next season of growth, they alter their reaction to gravity, becoming negatively geotropic, and growing up into vertical flowering shoots.

In typical stolons we do not know the circumstances in the shoot's development which determine this altered reaction to gravity. On the other hand in some plants without real stolons, but with shoots that under certain circumstances change their reaction to gravity, we do know the external factor which determines this change of reaction. Thus the German botanist Vöchting has observed in *Mimulus Tilingii* that the shoots in spring and when they begin to flower grow horizontally in a low temperature, and vertically in a high temperature. Similarly the Swede Lidforss showed that the shoots in different plants grow horizontally in a low temperature, but vertically in a high temperature (e.g. *Holosteum umbellatum, Lamium purpureum, Chrysanthemum leucanthemum, Stellaria media, Veronica hederifolia,* and *Anagallis arvensis,* &c.). By experiments with the first two of these species Lidforss showed that the changed direction of growth was dependent upon the changed sensitiveness to the stimulus of gravity, so that the shoots in a low temperature grew at right angles to the direction of gravity, while in a higher temperature they were negatively geotropic. We know nothing of how the change of sensitiveness arises, what it is in the plant that occasions the rising or falling temperature to alter its reaction; but recently some observations have been made which may perhaps help us to discover some of the links in the chain which brings about these changes.

We know that numerous roots, both primary roots and a great number of adventitious roots, so react to gravity that they grow vertically downwards; they are positively geotropic. If such a root be placed horizontally its continued growth makes it bend vertically downwards. The botanist Nemec has established the theory, which he supports by his anatomical investigations, that it is through the pressure of the starch grains on the cell protoplasm that the horizontally placed root learns, if I may use the word, the alteration of its position. Nemec has always found starch grains in the extreme tips of the roots in certain of the cells of the root-cap. Because the starch grains have a higher specific gravity than the cell-sap, they always sink down to the bottom wall of the cell and rest on the protoplasmic lining of this wall. When the root assumes a horizontal position the wall on which the starch grains have been resting becomes vertical, and the starch grains sink down on to what was formerly

the lateral wall, but has now become the floor. Nemec supposes that it is by the pressure which the starch grains now exert on the proto-plasmic lining of this wall that the root becomes aware of its altered position. How this actually happens it is impossible for us to understand; but if the theory proves to be true we have discovered one link in the chain of events, and that is at any rate a beginning.

In support of this theory may be mentioned the investigations of the German botanist Haberlandt on the direction of the stem in *Linum perenne*. The stems of this species always grow erect in the summer and are markedly negatively geotropic; but in the autumn when the tempera-ture has sunk to a certain point the shoots no longer grow vertically upwards, but proceed irregularly in various directions. If such plants are brought into the higher temperature of a greenhouse the shoots after some time again become strongly negatively geotropic and grow vertically upwards. Anatomical investigations showed that the autumn shoot, which had lost its sensitiveness to gravity, had no starch grains in its cells; but starch grains were formed when the plant was moved into the warmth, and since everything takes time, an interval elapsed before the starch grains were formed, and during this interval the stem showed no tendency to grow vertically upwards in the warmth; but as soon as the warmth increased the vital activities of the plant sufficiently to make it begin to form starch grains, the stem began to grow vertically upwards. Not until the starch grains were formed did the stems regain their old sensitiveness to gravitation.

These investigations show that there is very probably a relationship between the presence of starch grains and the alteration of reaction of shoots towards gravity. This brings us back to the experiments of Vöch-ting and Lidforss which showed that the shoots of certain plants are negatively geotropic in warmth but grow at right angles to gravity when the temperature is lower. This reaction explains how sensitiveness to gravity may alter with changes to temperature. Besides the plants mentioned by Vöchting and Lidforss many other species have horizontal shoots in the autumn (e.g. *Anthemis arvensis* and *Arenaria serpyllifolia*). It is perhaps along this line that we may hope to investigate the causes which brought about the origin of stolons.

We encounter here, as we always do when the question of new characters arises, which is the same question as that of the origin of new species, two hypotheses which we may call that of Darwin and that of Lamarck, even if these hypotheses at the present day are altered and more sharply defined than they were originally. We must consider whether the stolons, which are shoots with a changed reaction towards gravity, have arisen because of an internal unknown force operating by means of hereditary variation (or 'mutation' as it is usually called to-day), or whether they have arisen from shoots whose reaction has been altered

by the influence of such factors as their own weight, or a snow covering, affecting the shoots generation after generation, and at length gradually altering their internal economy, so that they continue to grow in the changed direction even after the factors which brought about the change no longer operate.

Several investigators are inquiring into the question of hereditary variation, into the hereditary characters, but such investigations miss the main point with which we are concerned, the origin of the characters in question, and only concern themselves with the transmission of characters which already exist. The question of heredity is being much more thoroughly investigated now than it was formerly; but of the origin of the characters, which is the main question, we know nothing; we know neither how nor when any given hereditary character came into being; we merely see that it exists. This is of course true of the much discussed 'new' characters which the Dutch botanist H. de Vries has found in part of the offspring of *Oenothera Lamarckiana*, a plant he has investigated thoroughly. Whether these characters are new, whether they arose in the course of H. de Vries's cultivation of this plant, or whether they had been present for hundreds or indeed thousands of years, we do not know for certain. For the fact that a given character has not been seen before does not necessarily mean that it has not existed before. It would be an extraordinary coincidence, one chance out of an infinity of chances, that a botanist should be present at the time when a character first came into existence. We can never be certain that a character not observed before is new. Of itself this fact is of no great importance: it would be of much greater importance if, in the course of our investigations of plants in which such sources of error as self-pollination and parthenogenesis were excluded, we could succeed in producing hereditary variations by known causes, if we could succeed, in fact, in producing hereditary variations by submitting the plant to definite influences. Whether we should ever succeed in doing this in the higher plants is a difficult question; but we are certainly justified in attempting to do so.

While in Darwin's hypothesis the inheritance of the characters, or of the variations, is the known fact and the origin of the variations is unknown, in Lamarck's hypothesis the origin of the variation is the known quantity and their inheritance the unknown quantity. It is just these 'conditioned' characters we have to deal with here, and we either know the causes of their origin, or we at least know how we must proceed to find out these causes; we also know that these characters are not inheritable in the ordinary sense of the word. The unknown, the undecided and difficult question is whether the presence of the conditioned characters throughout a long series of generations can so influence the organism that characters originally conditioned at length become hereditary, i.e. occur also when the causes necessary to their origin are no longer present.

Many facts in Ecology and Plant Geography are best explained by the help of this hypothesis. The hypothesis helps, too, in explaining facts I have used in characterizing life-forms. We do not know whether the hypothesis is true, but it has this great advantage that we know how to set to work to prove it, we know how to start the necessary experiments. We can cultivate plants experimentally throughout a long series of generations under conditions that originate certain characters which are not hereditary. Then we can find out, after the lapse of a long time, by cultivating the descendants of these plants, whether the characters will be present even if the conditions which brought them into being are no longer present. Some ten years ago I began experiments of this kind, but I gave them up again, for even granted that the hypothesis be true, such experiments would probably extend over a greater number of years than the lifetime of a single man, so that if the work is to be the affair of a private individual it will probably be done in vain. I proposed therefore eight years ago, and again later, the establishment of Phylogenetic Institutions, where experiments of this kind could be carried out independently of the lifetime of a single investigator. Such institutions would be best united to Botanic Gardens. Experiments like the one indicated above might be set on foot and I do not doubt that one day this will be done; for we can only make headway in solving the problem of the origin of characters, which is the same as the origin of species, by submitting Lamarck's hypothesis to experimental proof.

IV. CRYPTOPHYTES

Cryptophytes are plants whose buds or shoot-apices destined to survive the unfavourable season are situated under the surface of the ground, or at the bottom of water; the depth below the surface of the ground varies in different species.

The adaptation to environment, which consists in the buds destined to survive the unfavourable period being so situated that they are protected as well as they possibly can be against desiccation and sudden strong changes of temperature, is here attained in the most perfect manner, the buds being placed, not in the air as they are in Phanerophytes, nor on the surface of the ground as they are in Chamaephytes, nor in the soil-surface as they are in Hemicryptophytes, but completely buried in the soil at a distance from the surface, or at the bottom of water.

Since water plants, and albeit in a lesser degree, marsh plants, make well-defined groups, it is convenient to divide Cryptophytes into Geophytes, Helophytes, and Hydrophytes.

Geophytes include land plants whose surviving buds or shoot-apices are borne on subterranean shoots at a distance from the surface of the ground. They are particularly well adapted to live in districts with long

and marked dry periods; Geophytes are actually found predominantly in such districts as dry steppes, where they form a large component of the flora; but there are also a number of Geophytes that are adapted to and live in regions with a comparatively long period of vegetation, and where the unfavourable period is not a hot dry season but a more or less severe winter.

The Geophytes living in regions with a long dry period and short season of vegetation are adapted to finishing their epigeal life in a short period; as soon as the short, favourable, sufficiently humid season sets in they can at once begin and in a short time complete the development of the aerial shoots which bear foliage leaves and flowers. But in order that this can happen these organs must already have attained a comparatively high degree of development during their life under the ground, and this development must take place during the dry period. But since the plant during this season has no foliage leaves and therefore is not able to form the plastic material it needs, it must previously be furnished with sufficient stored-up nourishment. It is to meet this need that the plants are furnished with special organs for storage by means of which the plant can, during the dry season, develop leaves and flowers sufficiently far to make them ready to break forth as soon as the short favourable period begins. The rich floral display that appears at the beginning of spring is always emphasized as a characteristic feature in the flora of steppes.

The flowers often emerge before the leaves. We are familiar with this in various steppe plants cultivated in our gardens (e.g. *Crocus* spp.). The development of the flowers has to take place in absolute dependence upon the nourishment stored up during the last vegetative period; but this is usually true also of the species whose leaves and flowers develop at the same time, as may be demonstrated by removing the new leaves, which may be done without interfering with full development of flower or with seed formation.

Because of the shortness of the vegetative period, the formation of plastic materials and of the organs have taken place very early. In the short vegetative period the plastic materials are elaborated and in the long so-called 'resting period', which is really no resting period at all, but merely a time during which development is removed from our sight, the new organs are formed to the extent that only elongation in the individual cells is necessary to bring the leaves and flowers forth into the daylight. Since the nourishment formed in the vegetative period by means of the foliage leaves is not used till after the leaves are dead, Geophytes must possess organs in which plastic material may be stored. That is the reason for the peculiar feature of these plants, that they are furnished with the special storage organs which are so characteristic of them.

In some the food is stored in thick fleshy leaves which are packed close

together like the leaves of a bud, forming what is called a bulb; in others the store for the food is a short thick tuberous stem or tuberously swollen roots. We thus have three groups of Geophytes: Bulb Geophytes, Stem Tuber Geophytes, and Root Tuber Geophytes, all of which live preferably where there is a long dry period and a short period of vegetation, and even if some of them are met with in regions with a comparatively long favourable season they usually complete their aerial life in a short time.
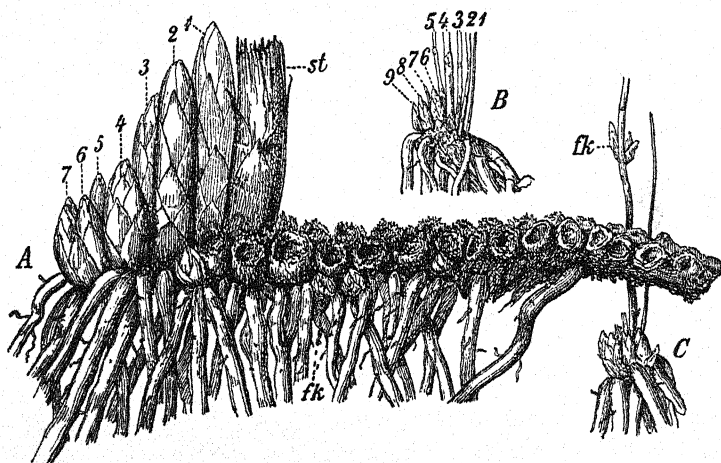

Fig. 38. *Asparagus officinalis*; Rhizome Geophyte; the subterranean stem of an older plant, A, and one of two younger plants, B and C; *st* in A is the lowest part of the last developed of last year's aerial shoots; to the right of this are seen the scars of the aerial shoots of the last three years; 1–7 in A and 6–9 in B are the buds which spend the winter in the earth; they are now about to grow into epigeal shoots. The young plant, C, has been planted comparatively deep—presumably too deep—in the earth; at some distance on the erect shoot, but still under the soil-surface, there are laid down some buds (*fk*) forming a new centre of growth higher up in the earth.

Besides these three groups of Geophytes we can recognize a fourth, namely Rhizome Geophytes, which are very likely just as well adapted to their life in the ground, but their underground stem is not nearly so extensively modified, differing indeed little from the underground stem of the Hemicryptophytes. Rhizome Geophytes are adapted to life preferably in regions which indeed have a severe unfavourable period, for example a hard winter, but have at the same time a long period of vegetation, so that they do not need to have a large amount of food stored up, and do not therefore need special organs to store it. The stems of Rhizome Geophytes are more or less elongated, and as a rule horizontal (Figs. 38 and 39).

As a fifth small group may be mentioned the Root Geophytes, which persist wholly or principally during the unfavourable season by means of buds on the roots, which are hidden in the ground and which are

protected by it, the shoot dying away at the beginning of the unfavour-
able period.

Although Geophytes seem to be well protected by being wholly hidden
in the ground during the unfavourable season, yet the influence of
drought can sometimes reach them there. In such cases we find that the
underground organs have the need of special protection. We recognize
amongst the underground organs of Geophytes a series of structures
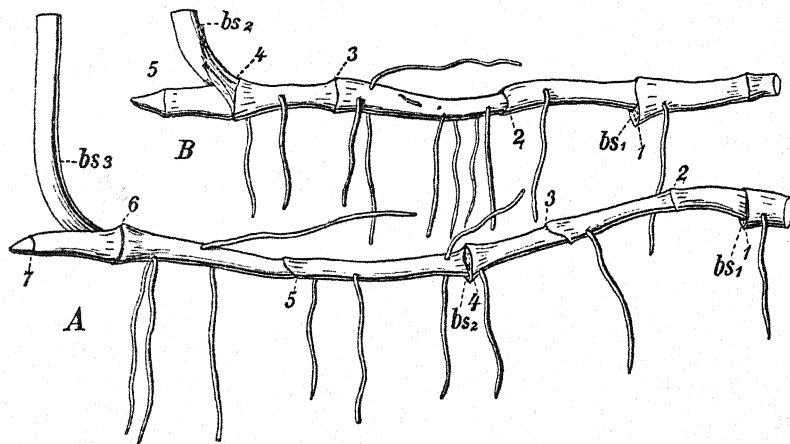specially designed to serve as a protection against drought. Thus in

Fig. 39. *Paris quadrifolia*; Rhizome Geophyte; the front part of two flower-bearing subterranean
stems; bs_3 in A and bs_2 in B is the lowermost portion of the erect flower-bearing aerial shoot; bs_1 and
bs_2 in A and bs_1 in B are scars of the flowering shoots of the preceding year; the subterranean stem,
which is a monopodium, is horizontal and lies several centimetres from the surface of the ground;
the winter buds are also at this level (7 in A and 5 in B).

Bulb Geophytes there are either especially formed protective leaves, or
the outermost leaves of the bulb already emptied of their food material
serve for protection. Thus in many Stem Tuber Geophytes (*Crocus* and
other *Iridaceae*) we find protective leaves enclosing the tuber. Other
Stem Tuber Geophytes protect their tuber from desiccation by develop-
ing in the periphery of the tuber a special protective tissue, notably
cork (*Arum, Solanum tuberosum*, &c.). Lastly other plants are protected
by the composition of their cell-sap, which prevents water being easily
lost, e.g. root tubers of ground Orchids, and many bulbs, &c., whose
cells are rich in mucus.

Since the buds of Geophytes are situated deep down in the earth
before they develop into aerial shoots, they have to break through a
layer of earth of varying depth. Even if the soil at the time when the
shoots sprout is soft and moist, yet the resistance it offers is usually so
great that the tender young growing plants and flower buds would not
be able to break through it without suffering damage were it not for

some special adaptation. We also find therefore among Geophytes different structural devices which serve to facilitate the growth of the shoots through the soil.

Some species grow with their shoot-apices not directed forwards, but the stem is bent slightly behind the apex so that the growing point is turned downwards or backwards, while the older and firmer part of the stem, which forms a bow, breaks a way through the soil, if I may use the expression, by putting its back into the work (*Anemone nemorosa, Eranthis*, &c.).

In others whose shoots are not thus bent the older and firmer leaves are packed tightly together around the shoot-apex forming a protection to the young and tender leaves, and sometimes also to the flowers, thus taking the first brunt of the shock from them; it is still however the growth of the shoot which is the force used in breaking through the soil. An example is *Fritillaria imperialis*. In other plants the leaves serve not only to protect the bud and to pave the way, but the driving force comes actually from the growth of the leaves (*Gagea* and many other Bulb Geophytes). In these plants the leaves are packed tightly together and protect the flower-bearing aerial stem, while it is growing up to the surface of the soil. The leaf-apices, which are tightly packed and as a rule have a specially dense structure, penetrate higher and higher up through the earth because the leaves grow at their base. When they reach the surface the leaves diverge from one another, and the flowering stem, which they have hitherto enclosed, now grows freely up into the air.
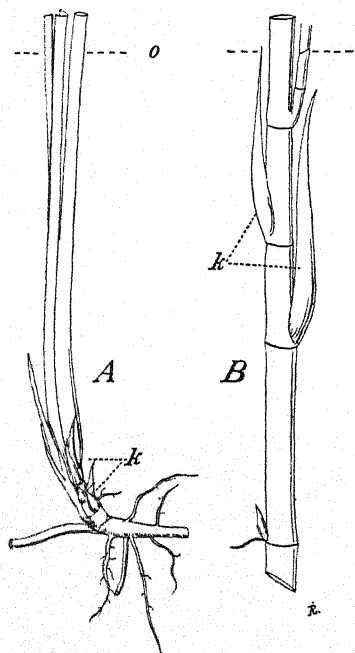
FIG. 40. A, *Calamagrostis epigeios*; B, land form of *Phragmites communis*; *k*, winter buds; *o*, soil-surface. ($\frac{2}{3}$)

23. **Rhizome Geophytes** have as a rule a more or less elongated, usually horizontal rhizome, which is almost invariably a sympodium composed of the lowermost horizontal portions of the individual shoots whose uppermost vertical parts project into the air and bear foliage leaves and flowers. If the rhizome be situated at a depth proper for the species the individual shoot in the first part of its life is transversely geotropic, growing at right angles to gravity, but it changes its reaction towards gravity at a certain time of its life and becomes negatively geotropic. We have already seen that this happens in Hemicryptophytes with subterranean stolons; but the peculiarity of Rhizome Geophytes, which

gives them their cryptophytic character, is that they are not only able, by change in the direction of growth, to attain the proper depth for their own species, but to place their winter buds at this depth, and not in the soil-surface like the subterranean stolons of Hemicryptophytes.

Examples of Rhizome Geophytes are: *Polygonatum multiflorum* (Figs. 45–8), *P. anceps, P. latifolium* and other species, *Paris quadrifolia* (Fig. 39), *Asparagus officinalis* (Fig. 38), species of *Cephalanthera, Epipactis, Listera, Neottia, Coralliorrhiza, Epipogon, Eriophorum alpinum* (Fig. 42), *E. polystachyum, E. gracile, Heleocharis palustris* (Fig. 44), *H. uniglumis, Scirpus compressus, S. rufus, Carex incurva, C. arenaria* (Fig. 43), *C. disticha, C. flacca, C. ericetorum, C. verna, C. acutiformis* and others, some Grasses (Fig. 40), *Maranta arundinacea* (Fig. 41), *Curcuma longa, Anemone nemorosa, A. ranunculoides, Dentaria bulbifera, Tussilago farfarus.*

Many Rhizome Geophytes can travel both up and down in the soil according to whether the rhizome is placed too deeply or not deeply enough, e.g. *Polygonatum multiflorum* (Figs. 45 and 48), *Paris quadrifolia, Asparagus officinalis, Cephalanthera rubra, Listera ovata, Juncus obtusiflorus,* and *J. filiformis.* When the rhizome-apices have arrived by the altered direction of growth

FIG. 41. *Maranta arundinacea,* a Rhizome Geophyte, the apices of whose rhizomes lie at a considerable depth; *a,* the mother rhizome of the right-hand plant was laid in the soil-surface, of the left-hand plant about 10 cm. below the soil-surface. From each of the mother rhizomes, *a,* there was given off an aerial shoot, *b,* which developed many roots in the soil-surface, *o,* from the bases of the radical leaves; from the axils of these leaves are developed several stolons, *c,* which grow vertically downwards to a depth of over 25 cm.; the stolon in the figure to the left, reaching the bottom of the box in which the plant was cultivated, was compelled to grow to one side. (½)

at a depth proper for the species, which is presumably the depth at which the plant thrives best under the circumstances, the rhizome again takes up a horizontal direction. This depth is different for the

different species and seems also to differ at different stages in the development of the same species. The depth perhaps also varies slightly with the external conditions.

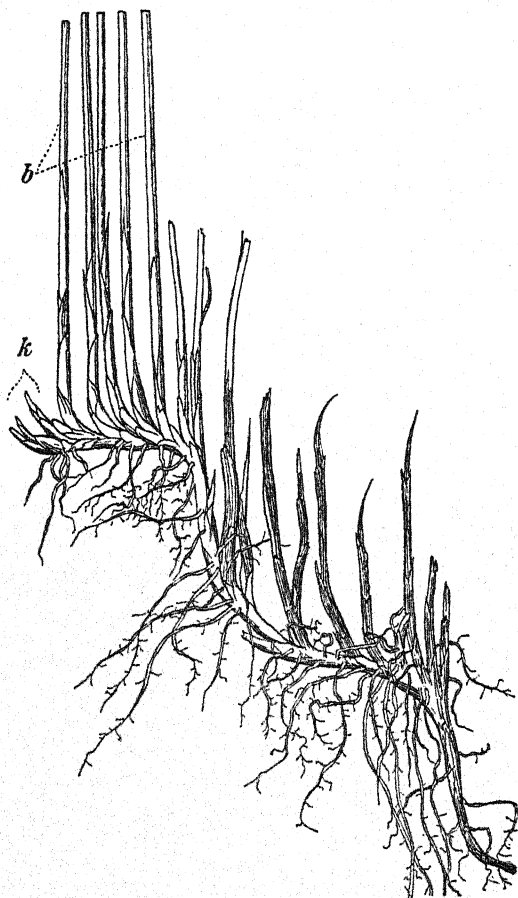In some species the rhizome is able to ascend when buried too deeply in the soil, but on the other hand it seems unable to descend, however high in the soil it is situated, provided that it is covered with soil, e.g. *Anemone nemorosa, Heleocharis palustris, Carex disticha, C. arenaria* (Fig. 43) and *Eriophorum alpinum* (Fig. 42). If on the other hand the rhizomes are laid bare and exposed to light they grow at once obliquely downwards until the apex is buried in the earth, where it resumes its horizontal growth; it is this process that produces the curious loop formations that we often see in *Heleocharis palustris* (Fig. 44) and other plants; *Anemone* often produces much smaller loops, and similar loops are met with also in Hemicryptophytes with subterranean stolons, e.g. *Achillea millefolium.*

That Rhizome Geophytes are able, by changing the direction of their growth, to take up their position at a definite depth can be demonstrated by planting the rhizomes at different depths; but it is a far more difficult matter to discover how rhizomes learn whether they are at a normal depth, or whether they are too high up or too low down in the soil. Only few experiments have been made with the object of elucidating this problem. I have carried out a series of experiments with *Polygonatum multiflorum* which, as before mentioned, belongs to the plants whose

FIG. 42. Rhizome of *Eriophorum alpinum*, a Rhizome Geophyte which has grown in a rapidly increasing layer of peat, ascending to bring its winter buds, *k*, to a suitable depth; the surface of the soil is a little above *k* (c. ¾).

rhizomes are able to attain a definite depth in the soil. At this, the normal depth, the rhizome is transversely geotropic and therefore grows horizontally; at a greater depth it becomes negatively geotropic and grows obliquely upwards (Fig. 48, B–C), while at a less depth it becomes positively geotropic and grows obliquely downwards (Fig. 45), until it again reaches its normal depth, where it becomes transversely geotropic and grows horizontally.

Of the external conditions which vary with depth, and which therefore may be able to make a change in the geotropic sensitiveness of the rhizome, the following may be considered: composition of the soil air (e.g. percentage of oxygen), water content of the soil, temperature of the soil, and the resistance which the erect portion of the shoot has to overcome in piercing the soil. Experiments showed however that none of these conditions determined the altered direction in growth of the rhizome at different depths. There thus appears to be no other course open for us than to suppose that the plant is able to become aware of its depth in the soil, not by means of a determining factor in the soil, a factor which would alter with the depth, but by means of a factor above the soil and with which therefore the plant would not come into contact before the upright portion of the shoot reached the soil-surface. Of such factors light is the first and foremost one to be discussed. The influence of the light might, I think, be due
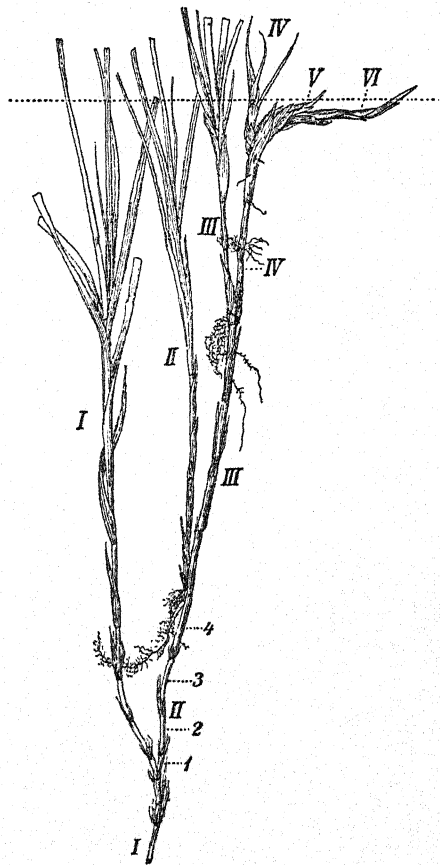

FIG. 43. *Carex arenaria*, a Rhizome Geophyte. The plant has become gradually covered with blown sand; instead of growing horizontally the rhizome portions of the shoots (II, III, and IV to the right) have grown nearly vertically upwards, thus saving the plant from being overwhelmed by the sand. The last developed generations, V and VI, which have reached the surface, bend over and grow horizontally; if the apex of the rhizome is laid bare it will then grow downwards into the sand. (c. ⅓)

to a kind of vital activity which enables the plant to measure the distance between the rhizome and the point where the erect portion of the shoot has reached the light. But if there is truth in this hypothesis we should be able to deceive the plant by substituting for the layer of earth a dark

layer of air; in other words we should be able to make the rhizome grow obliquely upwards even when situated high up in the soil, by taking care that the upright portion of the aerial shoot was not illumined immediately it reached the soil-surface, and that it did not reach the light until it

FIG. 44. *Heleocharis palustris*, Rhizome Geophyte, showing loop formation. The dotted line is the soil-surface. (*c.* ½)

had grown through the dark space containing no soil but only air. Experiments showed that the plant did actually behave in this way.

Some rhizomes were planted in the autumn at a depth of 5 cm.; over some of them zinc cylinders were placed. These cylinders, of which one was placed over each individual, were 8 cm. wide and 10 to 25 cm. high. The rhizomes which were beneath the cylinders, when they began to sprout next spring, had to grow up through the cylinder and did not

meet the light till they reached the edge of the cylinder. Each cylinder was covered with a cardboard lid, which later on, when the shoot reached it, was replaced by a cork through which a hole had been bored. The
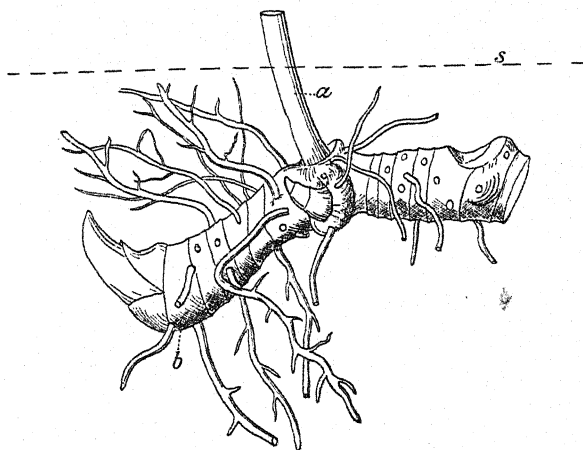
FIG. 45. *Polygonatum multiflorum*; a rhizome planted at a depth of 2 cm.; the terminal bud has formed an aerial shoot, *a*; the continuation shoot, *b*, has grown obliquely downwards; *s*, soil-surface. (⅔)
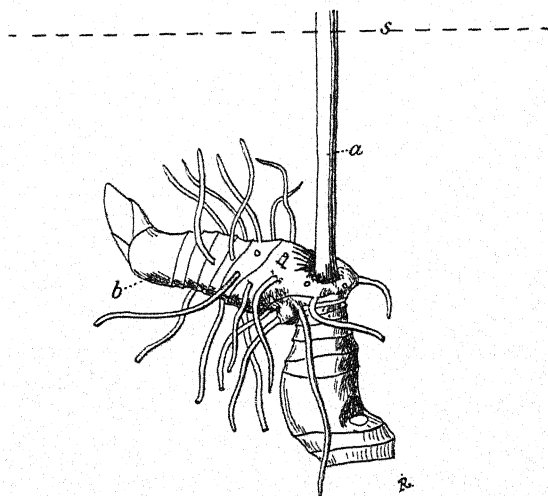
FIG. 46. *Polygonatum multiflorum*; a rhizome planted vertically with the terminal bud upwards and at a depth of 5 cm.; the terminal bud has formed an aerial shoot, *a*; the continuation shoot, *b*, has grown approximately horizontally. (⅔)

shoot grew through the hole up into the air and light; and in order to prevent the light entering the cylinder the hole in the cork was stuffed full of wadding wool. When the plants were taken up during the follow-ing August this is what was seen; in the plants whose aerial shoots had

not grown up through the cylinder the new segment of rhizome had grown approximately horizontally or slightly downwards; in the individuals whose aerial shoots had grown up through a cylinder and had not come into contact with light till reaching its edge, the new portion of rhizome was directed obliquely upwards (Figs. 47, 48, A). These plants then had been deceived; because of the darkness in the cylinder they had behaved as if their rhizomes were much deeper in the earth than they really were. From this it follows that the plant really determines its depth by means of the epigeal portion of the shoot, and that it measures the depth by the distance from the rhizome to the place where the epigeal portion of the shoot reaches the light; this distance will, of course, coincide in nature with the real depth.

Another and much more difficult question is this. By means of what internal vital activity in the plant does this measuring take place, and how does the result of this action alter the rhizome's sensitiveness towards gravity so as to make it grow in another direction? About this matter we know nothing. Neither do we know in what degree the other rhizome geophytes behave in the same manner as *Polygonatum multiflorum*.

24. **Stem-Tuber Geophytes** are distinguished by having one or several portions of the underground shoots tuberously swollen, serving as a storage organ, and bearing the bud or buds destined to survive the unfavourable season, while the rest of the shoot system, whether subterranean or epigeal, dies at the beginning of the unfavourable period.

Fig. 47. An experiment with *Polygonatum multiflorum* to find how the plant comes to know at what depth its rhizome lies in the soil; *s*, soil-surface; *t*, a zinc cylinder 25 cm. high, *p*, cork; *v*, wadding wool. See text. (*c. ⅓*)

The tubers may vary greatly in their origin, their duration, and their structure. In some, which form a connecting link with Rhizome Geophytes, the tuber is more or less elongated (*Polygonum viviparum*) (Fig. 50). In a number of Stem Tuber Geophytes the tuber is formed of the portion of the stem beneath the cotyledons, in some perhaps the neighbouring portions of the roots participate. Examples are: *Eranthis* (Fig. 51), *Cyclamen, Corydalis cava, Chaerophyllum bulbosum* (Fig. 52), *Bunium bulbocastanum, Tropaeolum brachyceras*, and other species,
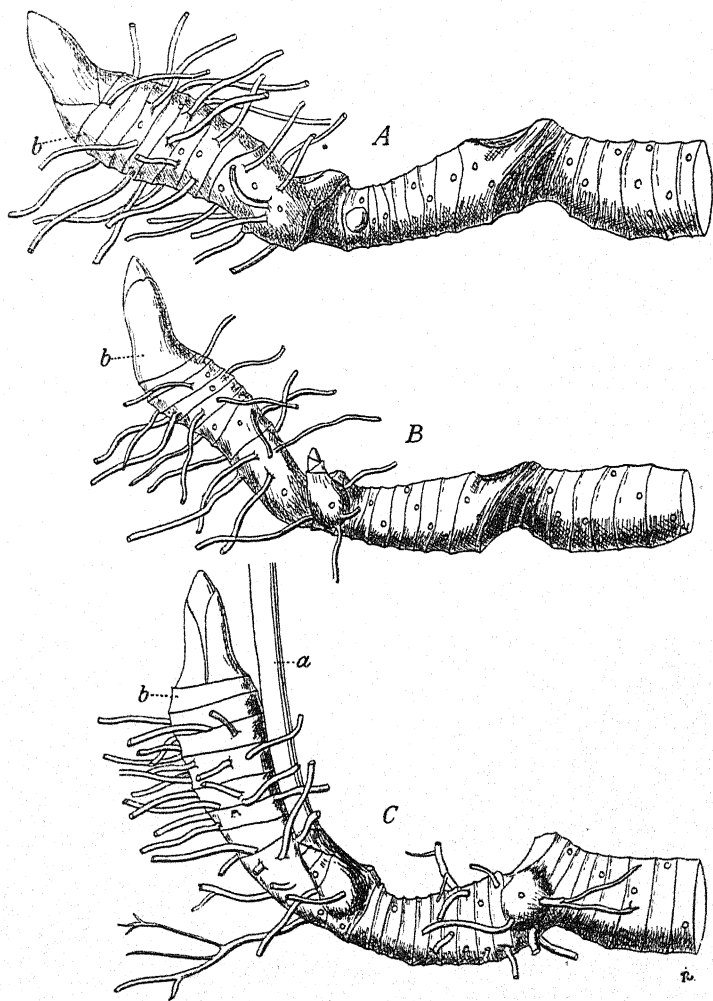
FIG. 48. An experiment with *Polygonatum multiflorum*; three rhizomes planted horizontally at different depths: A at 5 cm., B at 15 cm., C at 30 cm. In A the aerial shoot grew up through a cylinder 10 cm. high (see Fig. 47) so that it seemed to the plant that its rhizome was far deeper in the soil than it really was, and accordingly its continuation shoot, *b*, grew obliquely upwards, as did the continuation shoot, *b*, on the rhizomes B and C, which were deeply planted in the ground.

On the rhizomes that were planted at the same depth as A (5 cm.), but whose aerial shoots did not grow through a cylinder, the continuation bud grew horizontally or slightly obliquely downwards. ($\frac{2}{3}$)

Sinningia, Corytholoma, Begonia spp. (sub-genera *Huszia* and *Eupetalum*). In these plants the same tuber continues its life and serves as a starting-point for aerial shoots as long as the individual lives; all, or nearly all, of them are without means of vegetative reproduction and of determining the depth of the tuber in the soil; in some the position of the young tuber is determined merely by the position of the germinating seed, and
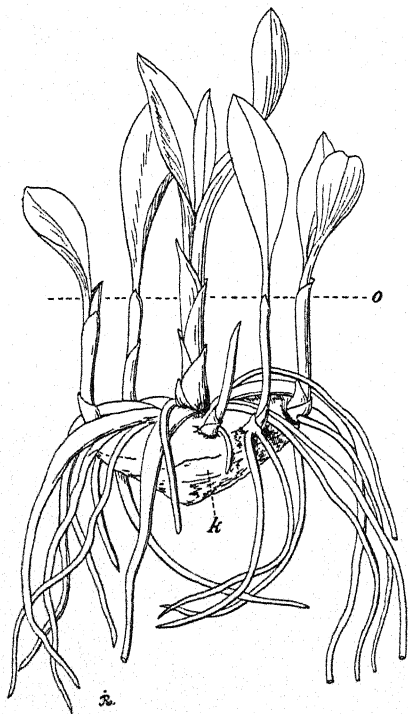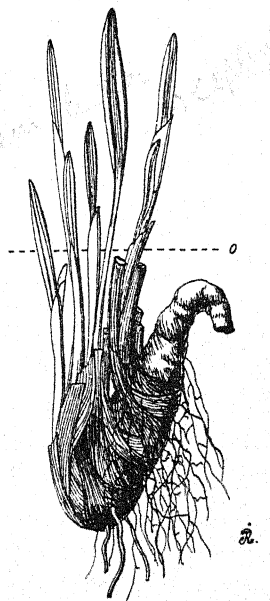

FIG. 49. *Biarum tenuifolium*; Stem Tuber Geophyte; *k*, tuber; *o*, soil-surface. (¾)

FIG. 50. *Polygonum viviparum*; Stem Tuber Geophyte, which by growing obliquely downwards comes to its proper depth in the soil. (¼)

in these it is only by 'hilling' that the tubers come to occupy a deeper position in the soil, e.g. *Sinningia, Corytholoma*, and *Begonia* species; in others when the seed germinates the young tuber is carried a longer or shorter distance down in the soil by geotropic growth at the base of the cotyledons; e.g. *Eranthis hiemalis, Chaerophyllum bulbosum*, and *Bunium bulbocastanum*, or the portion of the stem immediately above the cotyledons participates in the geotropic growth, e.g. *Tropaeolum brachyceras* and other species.

In other Stem Tuber Geophytes the tuber is formed by one or more of the internodes which follow after the cotyledons, and in these plants

the tuber usually lasts only for a year, a new tuber being formed every year as a starting-point for the following year's aerial shoot or shoots which develop with the help of the food stored up in the persisting tuber; the superfluous plastic material which the shoots formed during the period of growth is stored up in a new tuber formed of one or several
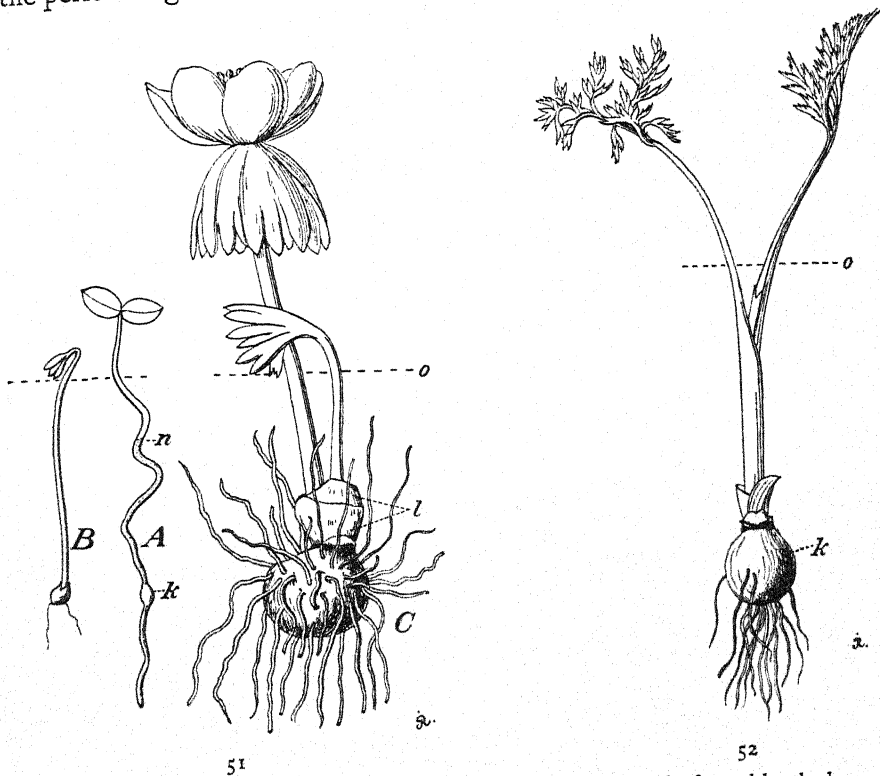
FIG. 51. *Eranthis hiemalis*, Stem Tuber Geophyte; A, seedling; *n*, tube formed by the base of the cotyledons; the bud is situated at the bottom of this tube at the apex of the young tuber (*k*). B, one-year-old tuber in the spring; C, an older plant at the flowering stage; *l*, tuber; *o*, soil-surface. (⅔)

FIG. 52. *Chaerophyllum bulbosum*, Stem Tuber Geophyte; young plant; *k*, tuber; *o*, soil-surface. (⅔)

of the shoot's lowermost internodes. Examples of these are *Colchicum*, *Methonica*, *Arum*, and other *Araceae*, *Crocus*, *Gladiolus*, *Ixia*, *Freesia* and other *Iridaceae*. In many of the *Iridaceae* which behave in this way there develops from the base of the individual bud a large fleshy turnip-shaped root whose essential function is doubtless water storage, but at any rate sometimes they also serve to pull the tuber lower down into the ground. Otherwise the species of this group have a very slight capacity for altering the position of the tuber in the ground; but some do certainly possess such a capacity, e.g. *Colchicum* and *Arum*. In *Colchicum* at germination the young tuber is carried down into the soil by a special device.
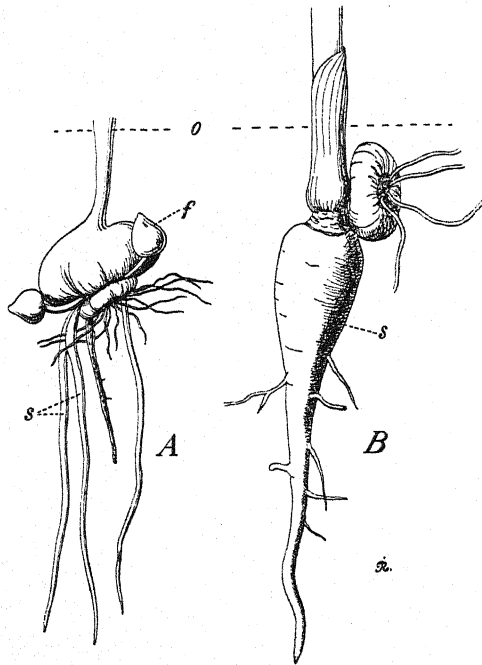
FIG. 53. Stem Tuber Geophytes. A, *Tritonia byalina*; *f*, stalked reproductive tubers; *s*, thick roots which are not, however, turnip-shaped. (⅔). B, *Gladiolus Colvillei*; *s*, turnip-shaped root; *o*, soil-surface. (⅔)
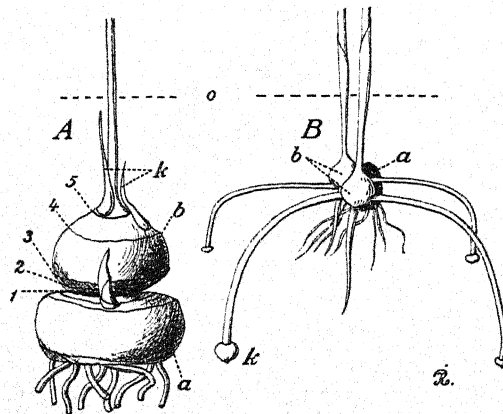

FIG. 54. Stem Tuber Geophytes. A, *Babiana plicata*; *a*, the old tuber; *b*, the young tuber, which is the lowest portion of the flowering shoot; 1-5, the five first leaves on *b*; 1, scale; 2-3, scales whose apices are like foliage leaves; 4-5, foliage leaves; above 5, there are three more foliage leaves; *k*, buds. (¼) B, *Ixia conica*; *a*, old tuber; *b*, the two young tubers; from the lowermost leaf axils on *b* there arise stolons which arch downwards ending in little tubers. (¼)

Several buds are often found on the tubers, but as a rule one of them is much stronger than the others, and sometimes this is the only one to develop. On stronger tubers one or two of the other buds usually

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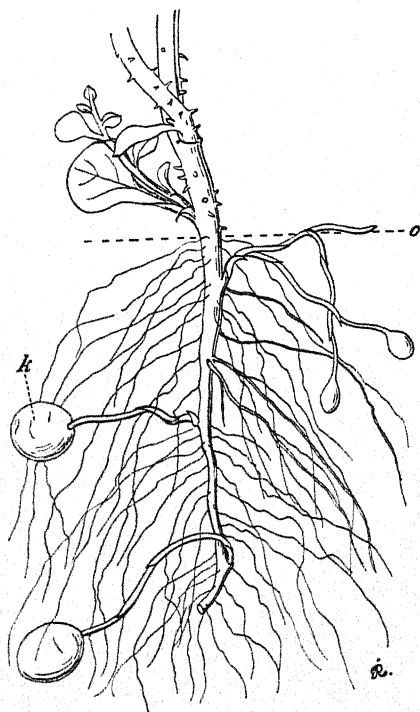
FIG. 55. *Ullucus tuberosus*; Stem Tuber Geophyte with new tubers, *k*, at the apex of the stolons; *o*, soil-surface. (†)
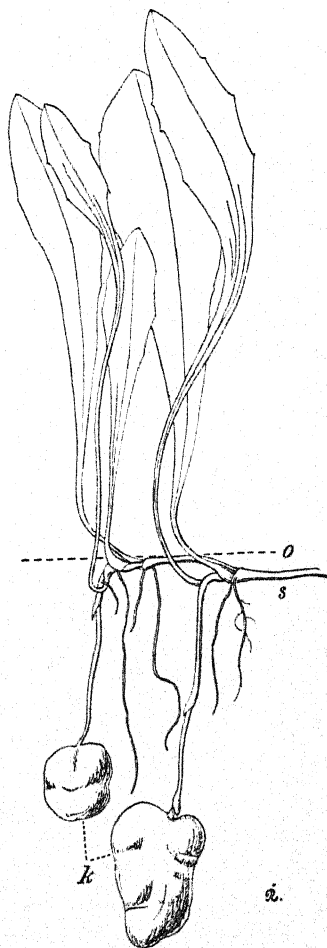
FIG. 56. *Crepis bulbosa*; Stem Tuber Geophyte with stolons whose apices develop into tubers; *o*, soil-surface. (⅔)

develop into weaker shoots, each of which produces a new but smaller tuber. In this way vegetative reproduction takes place. Sometimes these new tubers are separated from the mother tuber by means of stolons of varying length (e.g. species of *Tritonia* and *Ixia*, Fig. 54, B), and by this means distribution, though not extensive, takes place.

This leads us on to a third group of Stem Tuber Geophytes, in which a marked division of labour has taken place, the tubers not being formed at all on the aerial shoots, but only at the apex of subterranean stolons of varying length which arise either on the subterranean portions of aerial shoots or directly from the mother tuber. As examples may be
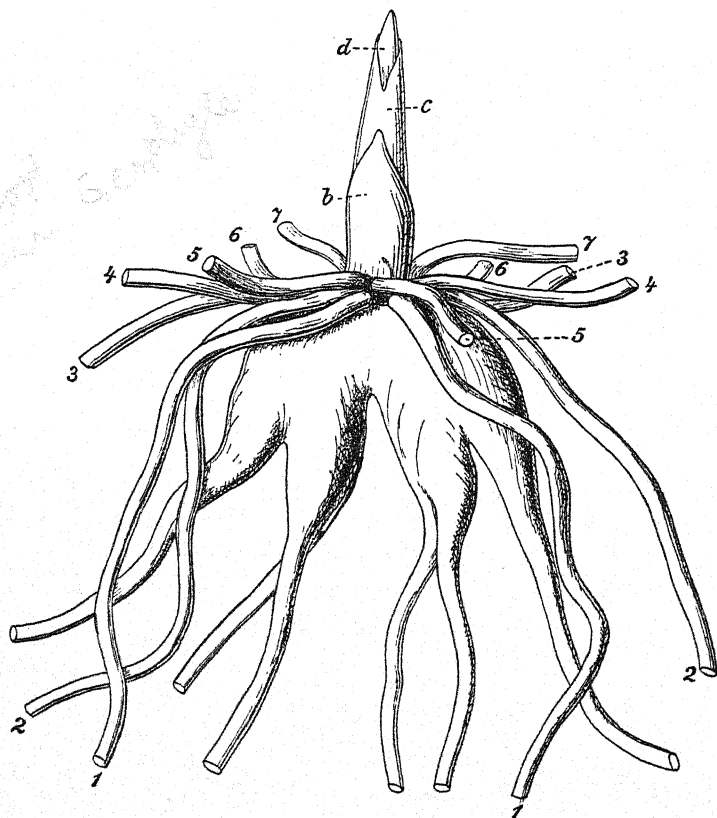

FIG. 57. *Orchis latifolius*, Root Tuber Geophyte, in the spring stage; the winter bud is sprouting. (⅓)

mentioned *Helianthus tuberosus*, *Solanum tuberosum*, and allied species, *Ullucus tuberosus* (Fig. 55), *Stachys affinis* and *S. palustris*, *Crepis bulbosa* (Fig. 56). As far as investigations have been carried out these plants seem to possess, within certain bounds, the capacity of regulating their depth in the soil by means of their stolons.

25. **Root-Tuber Geophytes.** In these the roots are swollen to form tubers or turnip-shaped bodies which serve as food stores. At the beginning of the unfavourable season the aerial shoots die right down. Only certain buds, together with the roots connected with them, survive the unfavourable season. We have been long familiar with this behaviour

Fig. 58. *Dichorisandra* sp., Root Tuber Geophyte; *a*, tuberously swollen rhizome from which the aerial shoot springs; *b*, continuation bud from whose more or less swollen axis there spring a number of tuberously swollen storage roots, *rk*; *o*, soil-surface. ($\frac{1}{3}$)

in *Orchis* (Fig. 57), and other *Ophrydeae*; *Dichorisandra* sp. (Fig. 58) behaves in the same way.

In the *Ophrydeae* the tubers live for only one year; the bud belonging to each tuber, when it shoots, uses up all the stored material, so that the tuber shrivels and dies, while the new continuation buds become furnished with their own tubers.

Tubers may get lower down into the soil by 'hilling', but the plants are also in some degree able to alter their position in the soil; if for any reason they find themselves too deep they can reach a higher level by elongating the internodes of the lowermost portion of the aerial shoot, which is situated in the soil, so that the continuation buds attached to this part of the stem are raised to a higher level in the soil (Fig. 59). Besides, at any rate in some species, sinking in the soil may be brought about by an individual bud being carried a little downward by obliquely downward growth of the part uniting the tubers with the mother axis. In *Herminium monorchis* (Fig. 60) the bud and the tuber belonging to it are carried a considerable distance from the mother plant because the part uniting the tuber with the mother axis is developed as a stolon.

26. **Bulb Geophytes** store their food in scale-like leaves or portions of leaves which are packed together like leaves in a bud; the persisting portion of the stem consists only of that part which bears leaves; the leaves surround those buds which in the next period of growth are destined to form new aerial shoots.

The numerous structural variations are well known. In some the bulb scales are complete leaves completely modified for storage, e.g. *Gagea, Lilium, Oxalis* spp. (Fig. 61), *Gloxinia, Achimenes*, and several other *Gesneriaceae* (Figs. 65–7), *Actinostemma* (Fig. 68). In others it is only the lowermost, often sheathing, portion of the foliage leaves (or scale leaves) which forms the bulb scales (e.g. *Allium, Ornithogalum, Galanthus, Leucojum, Narcissus*, &c.).

Bulbs are usually sympodial, the strong terminal bud of the bulb first developing into a flower-bearing aerial shoot when the favourable season begins and continuation taking place by means of lateral buds (Fig. 62), of which the one which arises in the axil of the uppermost of the radical leaves is usually by far the strongest. Examples occur especially in bulb-bearing *Liliaceae* and *Iridaceae*.

In others the bulb is a monopodium which every year produces a group of leaves, of which some become wholly or partially storage leaves, while the flower-bearing aerial shoots are lateral shoots (e.g. *Galanthus, Leucojum, Narcissus*, and other *Amaryllidaceae*).

In some species the bulb is made up of scales belonging to several seasons, and the food stored up in a scale belonging to one vegetative period is not used by an aerial shoot during the following vegetative period,
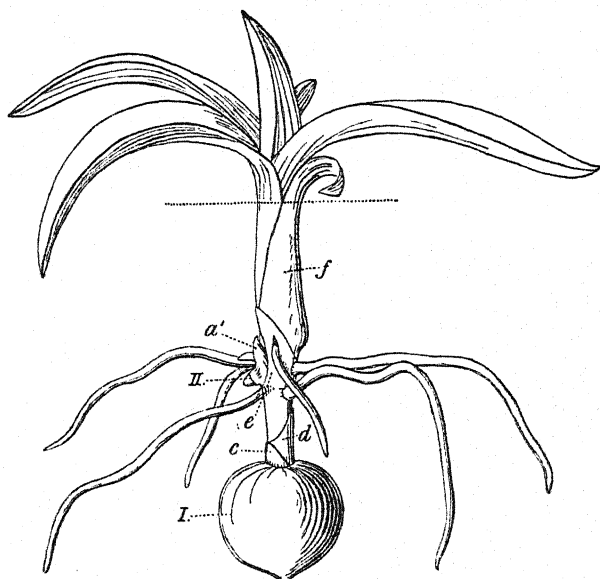
FIG. 59. *Orchis morio*, Root Tuber Geophyte; a plant in the spring stage. The continuation bud for the following year is already laid down, *a'*, and the tuber belonging to this bud, II, is about to grow out; the long dotted line is the soil-surface.
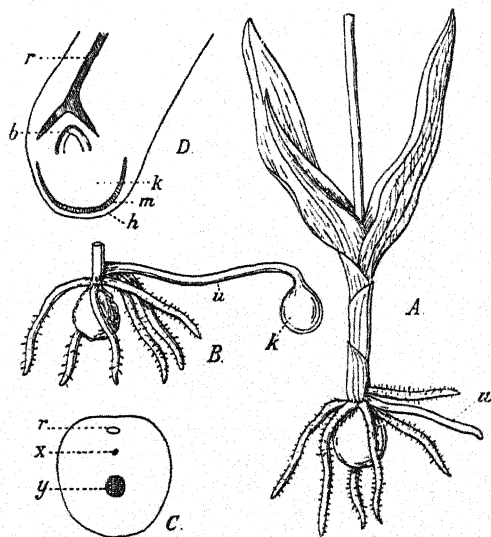

FIG. 60. *Herminium monorchis*; Root Tuber Geophyte. A, the lowermost portion of a flowering plant in June; from the base of the stem spring six adventitious roots (with root-hairs); the stolon, *u*, by means of which the new tuber is separated from the mother plant, is growing out. B, base of A after the new tuber, *k*, has been formed at the end of the stolon, *u*. (†). C, magnified transverse section of a stolon; *r* = *r* in D; *x* and *y*, vascular bundles. D, magnified longitudinal section through the apex of a stolon at the time of formation of the new tuber *k*; *b*, winter continuation bud; *r*, narrow canal which runs through the stolon and opens near the mother plant; it is by means of this tube alone that the continuation bud is connected with the air in the soil.

but during the one following that, or later still (e.g. *Ornithogalum nutans*).
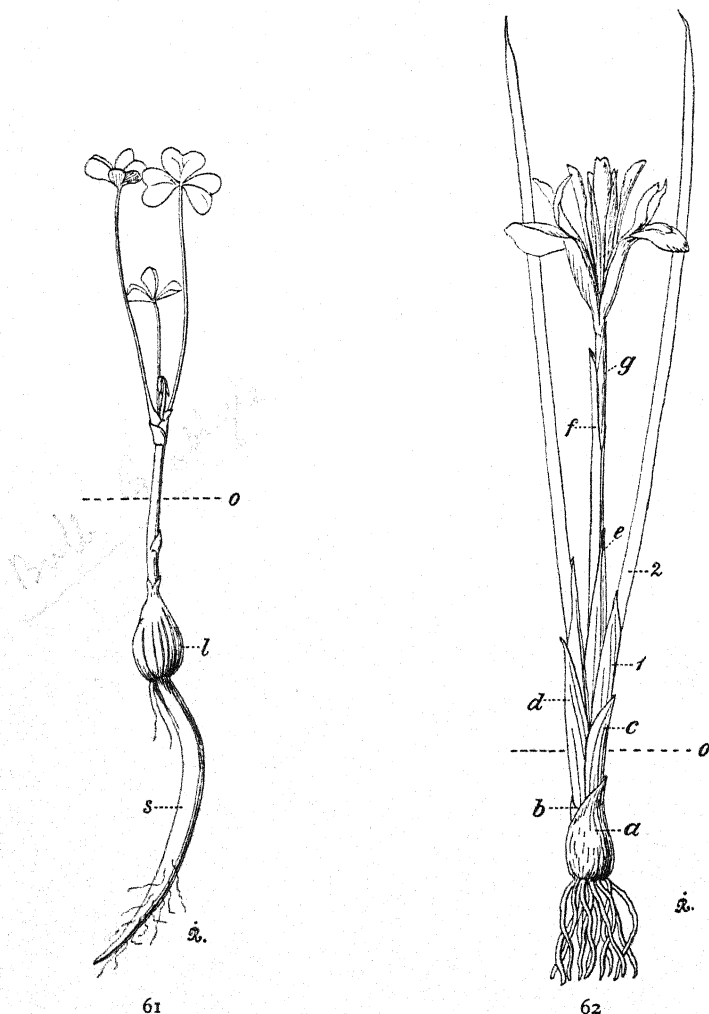Usually, however, the food stored during a period of growth is used by the

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FIG. 61. *Oxalis cernua*, Bulb Geophyte; *s*, sap-root; *l*, bulb; *o*, soil-surface. (⅔)

FIG. 62. *Iris bistrio*, Bulb Geophyte; *a–g*, the leaves of the flowering shoot (Nos. 3–9); the first and second leaves of the shoot, which were developed during the last period of growth, are dead; *a* is a storage leaf which also was developed during the last period of growth and is now partially empty of its food; in the axils of the fifth and sixth leaves, *c* and *d*, are lateral shoots each of which begins with a scale leaf, 1, and then makes a foliage leaf, 2, and within this a storage leaf corresponding with *a*. (½)

next year's aerial shoot, so that only one set of fresh storage leaves is present
in a bud (e.g. *Ornithogalum umbellatum*). In others again the developing
aerial shoot uses the food stored in its own lowermost leaves, which are
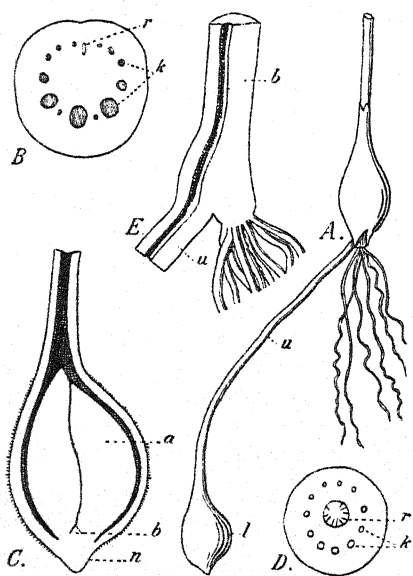
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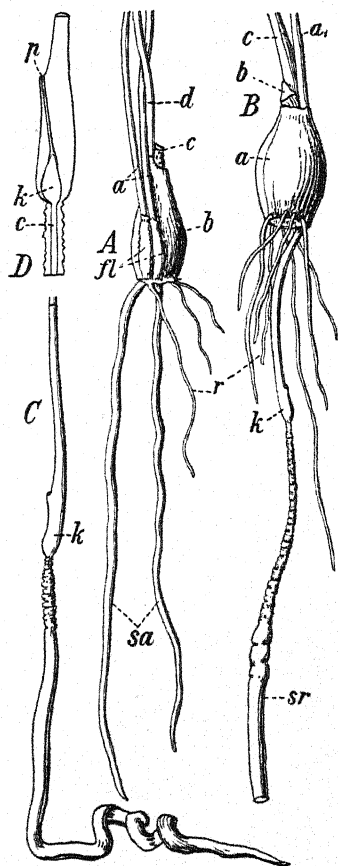
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FIG. 63. *Tulipa silvestris*, Bulb Geophyte. The new bulb, *l* in A, is being carried deeper into the earth by means of a slender stolon, *u*, in whose swollen end it arises. ($\frac{1}{4}$). B, transverse section through the stalk-like sheath of the foliage leaf; *r*, air canal; *k*, vascular bundles. ($\frac{10}{1}$). C, longitudinal section through the apex of a stolon with the new bulb, which connects with the air solely by means of a narrow canal which runs through the stolon and is continued up through the sheath of the foliage leaves of the mother bulb; the opening of this sheath is above the soil-surface. ($\frac{3}{1}$). D, transverse section of the stolon; *r*, air canal; *k*, vascular bundles. E, longitudinal section through the uppermost portion of a stolon *u*, and the lowermost portion of the sheath of the foliage leaf, *b*; the continuation of the air canal is seen running completely through the section.

FIG. 64. *Ornithogalum nutans*, Bulb Geophyte; example of a plant in which the buds are dragged down in the soil by means of the roots. A, a young bulb with two small daughter bulbs, *fl*, each with a foliage leaf, *a*, and each with a long rather slender sap-root, *sa*. ($\frac{1}{1}$). B, a similar bulb with only one daughter bulb, *k*, which by the contraction of the sap-root belonging to it, *sr*, has been drawn down into the soil; *a₁*, foliage leaf of the daughter bulb which is wedged in between the mother bulb and its leaf, *a*, in whose axil the daughter bulb has been situated. ($\frac{1}{1}$). C, daughter bulb with its sap-root and the lowermost portion of the foliage leaf. ($\frac{1}{1}$). D, longitudinal section through a daughter bulb; *p*, the opening of the sheath of the foliage leaf, leading through a narrow canal down to the bud, *k*. ($\frac{2}{1}$)

differentiated and filled with food material before the development of the epigeal flower-bearing portion of the shoot (e.g. *Gagea*).

In some species the bulb has no other protection than that afforded by the old scales which have become mere pellicles (e.g. *Ornithogalum*, *Gagea*, *Allium*, &c.). In others each new shoot, or in a monopodium each year's increment, begins with one or more membranous but firmly constructed protective leaves (*Tulipa*).
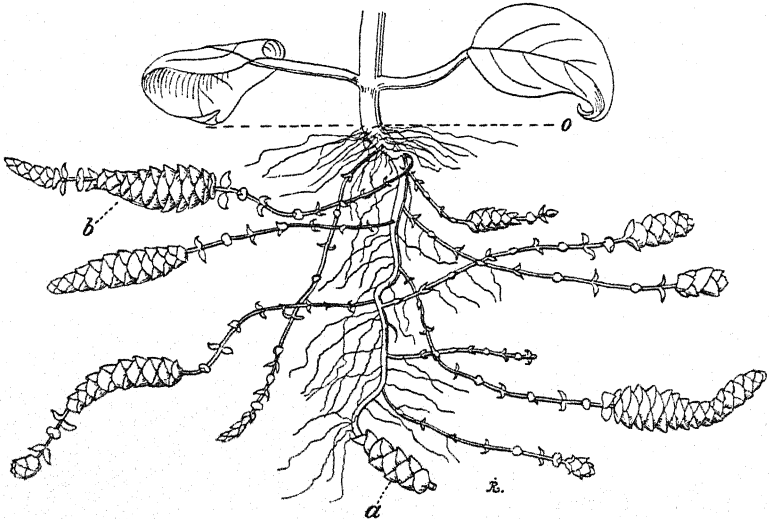

FIG. 65. *Tydaea Lindeniana*, Bulb Geophyte with catkin-like bulbs at the end of slender stolons. The terminal bud on the mother bulb, *a*, has grown out into an aerial shoot with foliage leaves and flowers; the underground portion of this shoot bears scale-leaves whose axillary buds grow out into stolons of varying length and form elongate bulbs (*b*) at their extremities, the tightly fitted leaves becoming thick and fleshy and packed full of food material. ($\frac{2}{3}$)

Most have no power, or next to none, of altering their position in the soil; growth carries them indeed gradually a little higher up, but 'hilling' increases their depth again. Some, like *Galanthus* and *Leucojum*, can, if they have sunk too deep in the soil, rise higher up again by interposing an elongated shoot-portion between the old and the new parts of the bulb. In many species of *Allium* the small daughter buds are carried on stalks to a higher level in the soil, where they presumably find the depth better suited to their size. In certain species of *Tulipa*, e.g. *T. silvestris* (Fig. 63), especially in young individuals, the young bulb is carried to a varying distance from the mother plant by a stolon, and the direction this stolon takes is within certain limits dependent on the depth of the mother bulbs, so that these plants possess a means of, at any rate partially, determining their depth in the soil. There are also species of *Oxalis* that can change their position in the soil.

In many species contraction of the roots can draw the bulbs down: in

Ornithogalum nutans (Fig. 64) the small daughter bulbs are carried by this means away from the mother bulb.

Vegetative reproduction takes place in all these species, the older plants developing, besides the new bulbs, also one or more reproductive bulbs. When these reproductive bulbs, either by the contraction of the roots, or by means of stolons, are carried away from the mother plant, vegetative distribution also takes place. Examples of this have been mentioned in *Ornithogalum*, *Allium*, and *Tulipa*; bulb-bearing *Gesneriaceae* behave in this way, and also *Actinostemma*.
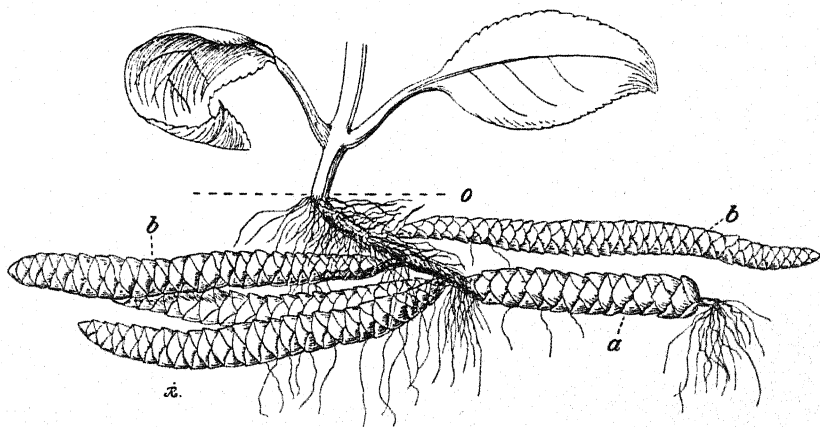

FIG. 66. *Isoloma pictum*, Bulb Geophyte; with long catkin-like bulbs. Development as in *Tydaea Lindeniana* (Fig. 65); *a*, mother bulb; *b*, new bulb; *o*, soil-surface. (⅔)

A great many *Gesneriaceae* (Figs. 65–7), viz. genera in the group *Gloxinieae*, and some genera in the groups *Kohlerieae* and *Bellonieae*, have underground stolons of varying length, ending in comparatively long cylindrical catkin-like structures which, in spite of their deviating form, can be referred to as bulbs (*bulbus articulatus, propagulum squamoso-amentaceum*): these bulbs are usually made up of a great number of small scale-like storage leaves which are packed tightly together on a slender axis. The species in question are native of Tropical and Sub-tropical America, and to judge by the manner in which they behave in our greenhouses, the epigeal portion of the plant dies in the dry season, the vegetative organs of the plant surviving this period solely by means of the bulbs which are buried in the soil. In the next period these bulbs send out new aerial shoots, and from the underground portion of these there arise new axillary stolons which bear scales and terminate their growth by the formation of a bulb. Such bulbs may also sometimes be formed on the epigeal portion of the plant, for example in the axils of prophylls (Fig. 67), afterwards descending to the ground.

In *Actinostemma* (*paniculatum*?) (Fig. 68) belonging to the *Cucurbitaceae*

the approximately spherical bulb consists of a collection of tuberous storage leaves; the terminal bud of this bulb grows out into a climbing, or under certain circumstances a prostrate, aerial shoot in whose leaf axils arise slender shoots with rudimentary leaves. The shoots grow downwards and are often branched, and the ends of the shoots often reach the ground, where the apex develops into a bulb. Some of the shoots however grow up from the ground again without forming a bulb. In these species considerable vegetative distribution can take place.

27. **Root Geophytes.** These plants, as I understand them, persist through the unfavourable season exclusively or principally by means of
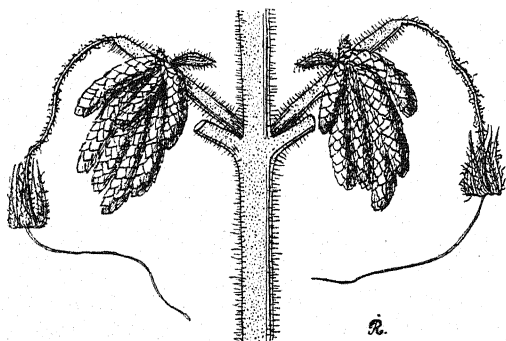

FIG. 67. *Achimenes cordata*, Bulb Geophyte. Fascicles of catkin-like bulbs are formed in the axils of the prophylls; the corolla has fallen away and the uppermost portion of the flower stalk has shrivelled up; the lowermost portion which bears the bulbs is fresh and turgid. (⅔)

buds situated on the persistent roots, while the rest of the plant dies at the beginning of the unfavourable season. *Cirsium arvense* is an example; *Chimaphila uniflora* might perhaps also be classed here; its epigeal shoot certainly does last through the winter, but as it bears no continuation bud it has no direct significance for the plant's capacity to survive the unfavourable season. In this respect it behaves like the aerial shoot in some species of *Rubus*.

There are certainly only a very few species which are typically Root Geophytes, surviving the unfavourable season solely by means of root-buds. On the other hand there are a great many species (*Linaria vulgaris, Rumex acetosella, Sonchus* spp. &c., &c.), which, according to our classification, should be classed among the Hemicryptophytes, but in which the bud formation on the roots is so common that one might suppose that those shoots which have already reached the soil-surface, or even a higher level, might die completely in the unfavourable season without the individual life being threatened, the plant surviving solely by means of the root-buds. In climates that are very unfavourable for Hemicryptophytes these species might perhaps occur as Cryptophytes, viz. Root Geophytes.
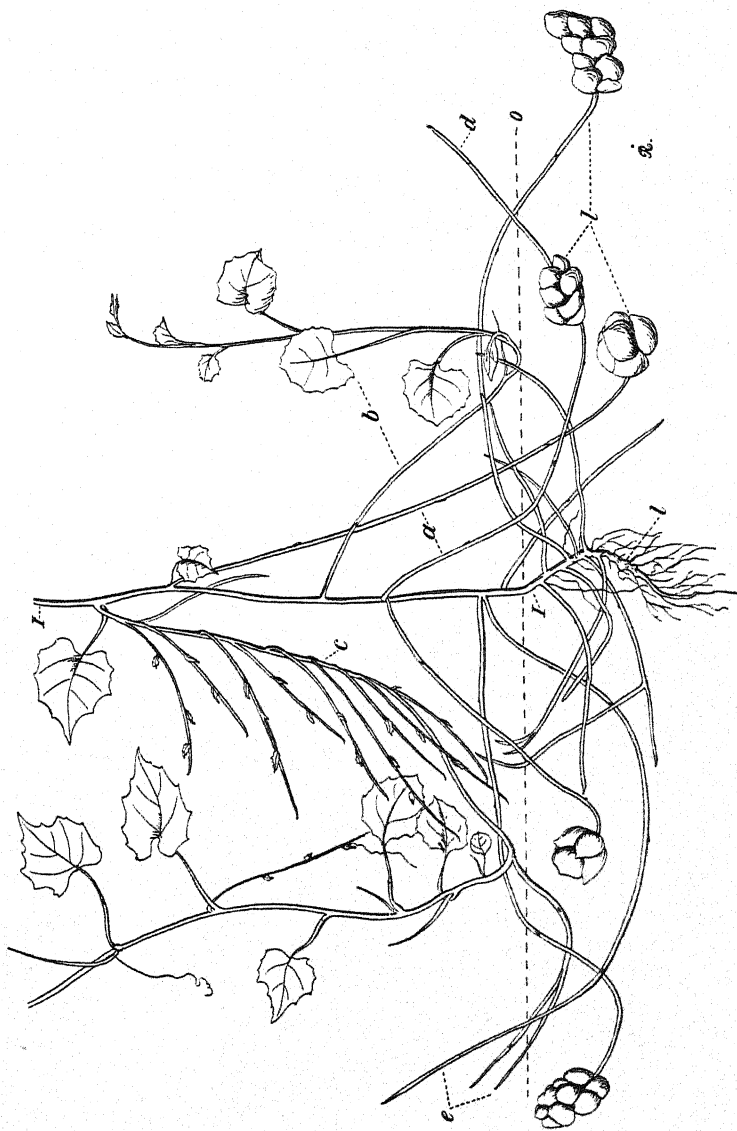
FIG. 68. *Actinostemma* sp. (*paniculatum?*), Bulb-Geophyte. The bulbs, *l*, which consist of a number of tuberously swollen leaves, are formed at the apex of elongated aerial shoots, *a*, which bear foliage leaves and grow downwards. These shoots eventually reach and penetrate the soil where the apex develops into a bulb, the internodes of the stem remaining short and the leaves swelling up and becoming full of food material. (½)

28. Helophytes. By Helophytes I mean those Cryptophytes which exclusively, or at any rate chiefly, grow in soil saturated with water, or in the water itself, from which the leaf- and flower-bearing shoots emerge. Helophytes do not therefore include all the plants ordinarily
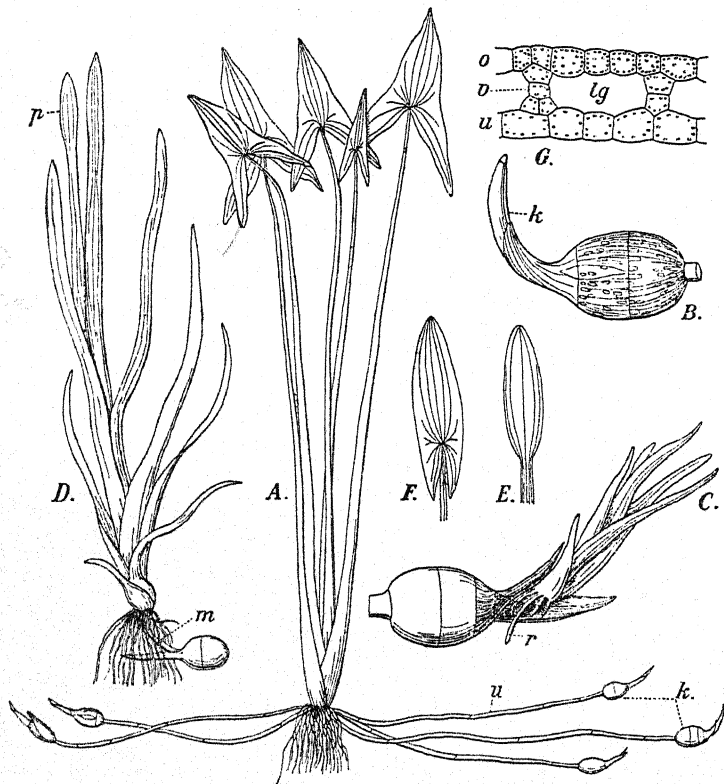

FIG. 69. *Sagittaria sagittifolia*, Helophyte. A, young plant not ready to flower, its leaf blades standing above the surface of the water, and long stolons, *u*, with tubers, *k*, at their apices, each tuber bearing a winter bud. (*c.* $\frac{1}{4}$). B, tuber with winter bud, *k.* (*c.* $\frac{1}{4}$). C (*c.* $\frac{3}{4}$) and D ($\frac{1}{4}$), tubers in the spring stage; the bud is growing out to form a new plant whose first leaves are ribbon-like and submerged; later on such long leaves are produced that they reach the surface and begin to develop laminae (*p* in D); these imperfect laminae, E and F, float on the surface of the water; after that perfect leaves are developed whose laminae stand above the water surface (A). G, part of a transverse section of a sub-merged leaf; *lg*, air chambers. (*c.* $\frac{100}{1}$)

known as marsh plants, but only those of them which are Cryptophytes; i.e. they are able to make use of a quality of the environment for pro-tecting their surviving buds, which are situated in the water or in the saturated mud at the bottom of the water. Examples are *Typha*, *Spar-ganium*, *Cyperus*, *Scirpus*, *Cladium*, *Sium*, *Acorus calamus* (Fig. 70), *Phragmites communis*, *Alisma plantago*, *Sagittaria sagittifolia* (Fig. 69), *Ranunculus lingua*, &c. Many Hemicryptophytes affect swampy places,

but this does not make them Helophytes, for their persisting buds are situated in the soil-surface. Such Hemicryptophytes may perhaps under special climatic conditions occur as Helophytes because the buds in the soil-surface die without the individual perishing, regeneration taking place by buds which are situated in the soil on old parts of the shoot, and which ordinarily play no part in the plant's life. The boundary between
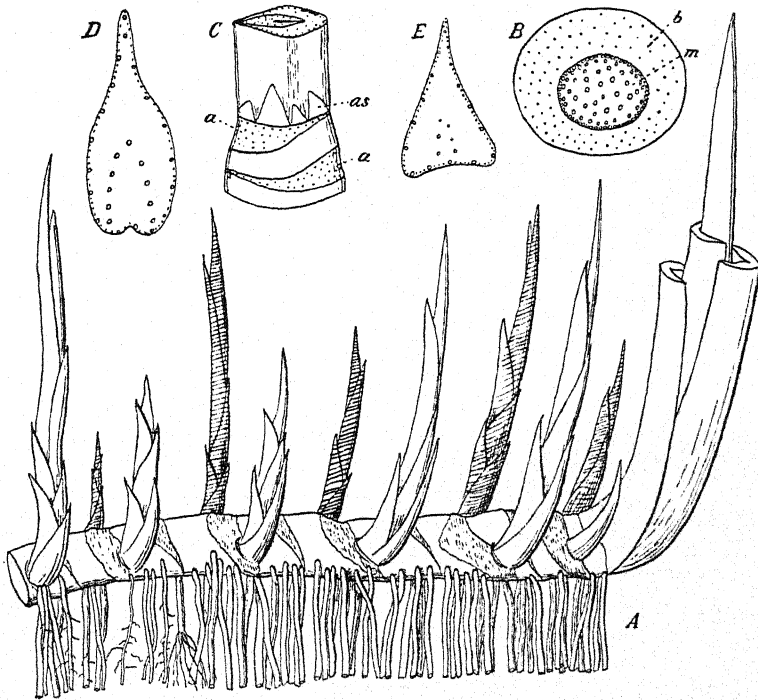

FIG. 70. *Acorus calamus*, Helophyte, A, with horizontal rhizome and two rows of winter buds or young shoots. B, D and E: transverse sections of a rhizome (B), aerial stem (D), and sheathing leaf (E); C, apex of a rhizome with terminal bud, whose leaves are cut off just above their bases; *a*, leaf scar; *as*, small scales in the leaf axils.

Helophytes and Hemicryptophytes which grow on wet soil is indistinct for another reason. It often happens that when the winter buds are laid down in the soil-surface, and when we should therefore expect the plant to be a Hemicryptophyte, the buds become submerged because of the rise in the level of the water during the autumn, and are thus protected throughout the winter like buds that are laid down in water from the very first.

Helophytes have usually elongated, horizontal, transversely geotropic rhizomes or stolons like Rhizome Geophytes: imperceptible gradations unite the two groups, many Rhizome Geophytes being able to grow as Helophytes and vice versa.

The rhizomes are ordinarily buried in the mud at the bottom of the water, but where the bottom slopes steeply, as it does along banks, it often happens that rhizomes growing horizontally from the banks project into the water, becoming exposed to the light; they then grow obliquely downwards into the water and again reach the bottom. This behaviour
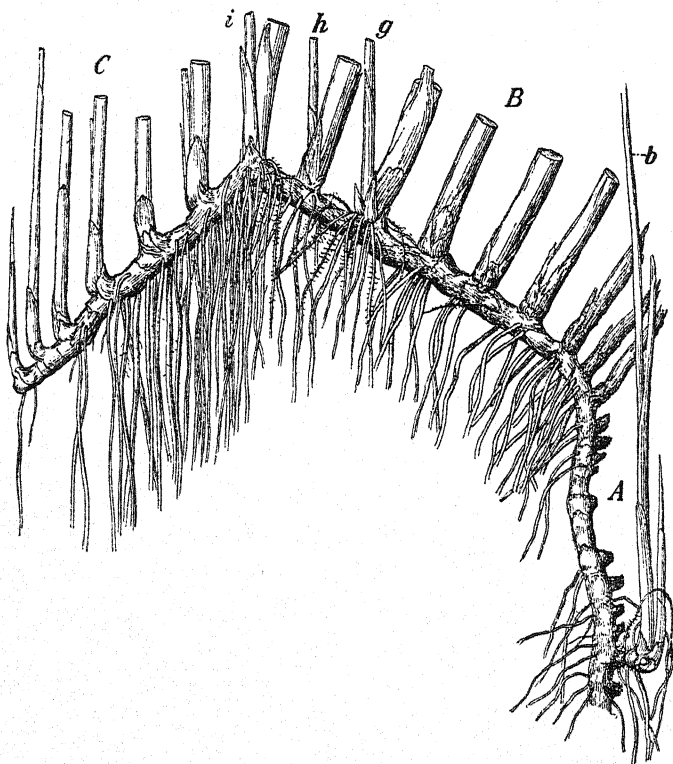

FIG. 71. *Juncus obtusiflorus*, Helophyte; a rhizome from the outermost part of a community growing in water. The vertical part, A, has originally been approximately horizontal, but at one time became loosened from the soft mud and tilted slightly upwards, whereupon part B grew out nearly horizontally, doubtless under the mud; after that the rhizome again became tilted up and came out of the mud into the water, where part C, exposed to the light, grew very obliquely downwards. Meanwhile the shoots *b*, *g*, *h*, and *i*, have grown out. (*c.* ½)

can also be observed in *Juncus obtusiflorus* (Fig. 71), *Cladium mariscus* (Fig. 72), *Scirpus lacuster* and *Typha* sp. (Fig. 73). It is not certain whether this downward growth depends upon the fact that these rhizomes are negatively heliotropic, or whether it takes place because they are positively geotropic in the light. In the experiments I made to elucidate this problem the rhizomes that were placed freely in the water certainly grew obliquely downwards in the dark also. This may signify that when they are free in the water even in the dark they are
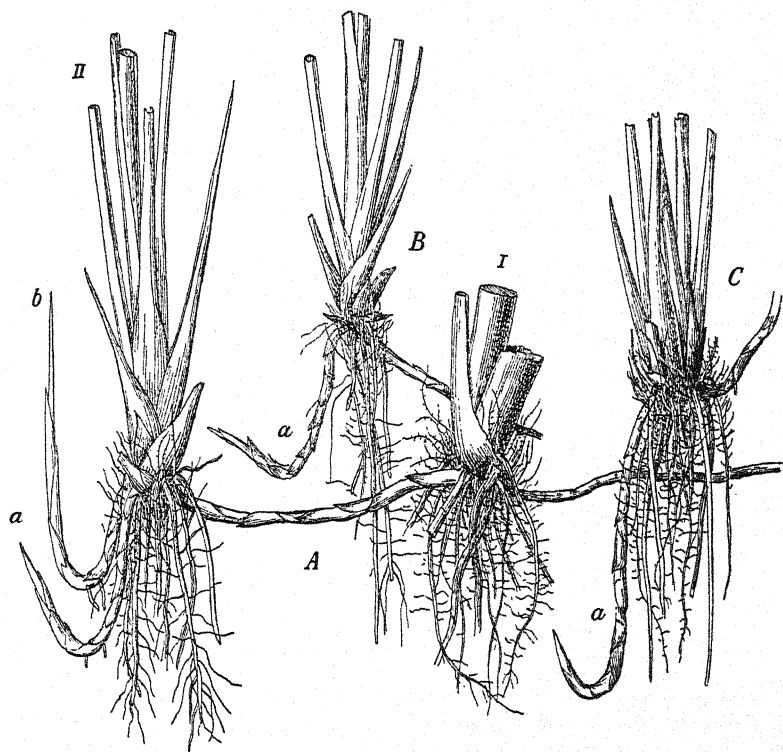
FIG. 72. *Cladium mariscus*, Helophyte; the youngest part of three rhizomes from the side of a community by open water; the rhizomes *a* exposed to the light grow almost vertically downwards. (*c.* $\frac{1}{3}$)
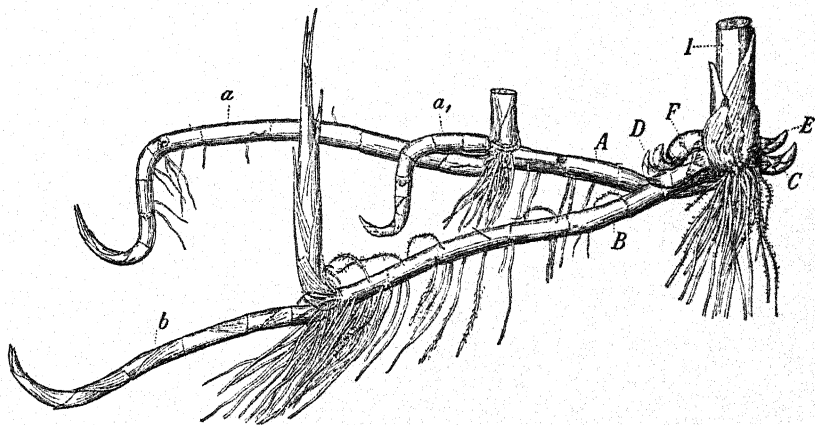
FIG. 73. *Typha latifolia*, Helophyte; the rhizome of a plant which has grown at the outer edge of a community; shoot B has grown obliquely downwards following the sloping bottom of the pond; shoot A has originally grown in the same direction, but before it became rooted suffered some kind of injury at its base; because of its lighter weight it has then been tilted higher up in the water, where it was exposed to the light, which has made the apices of the young shoots, *a* and a_1, grow vertically downwards. (*c.* $\frac{1}{6}$)

LIFE-FORMS OF PLANTS

positively geotropic; but since the aerial shoots which developed during my experiments had to be directed up through the covering used for

FIG. 74. *Potamogeton alpinus*; rooted water plant with winter buds. The shoot was pressed against the bottom by the force of the stream, and in the axils of each of the lower leaves a short stolon has then developed with the winter bud at its apex. (¼)

excluding the light, it was difficult completely to prevent the access of light to the rhizomes. I do not think it safe to conclude anything from my experiments, especially since the results of my observations are
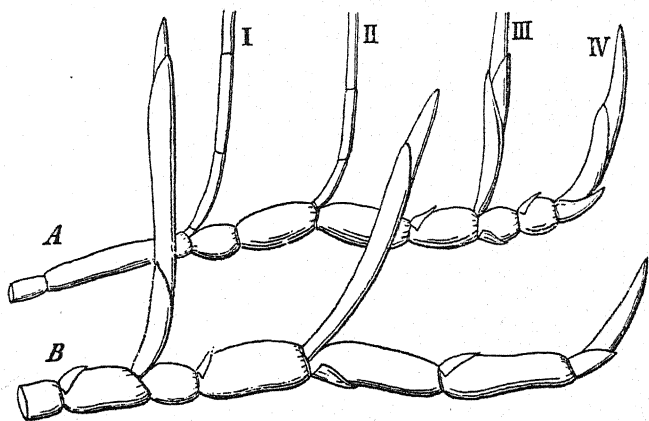
FIG. 75. *Potamogeton lucens*; rooted Hydrophyte; the apex of two rhizomes which survive the winter with some tuberously swollen joints; A with two (III and IV), B with three winter buds. (½)
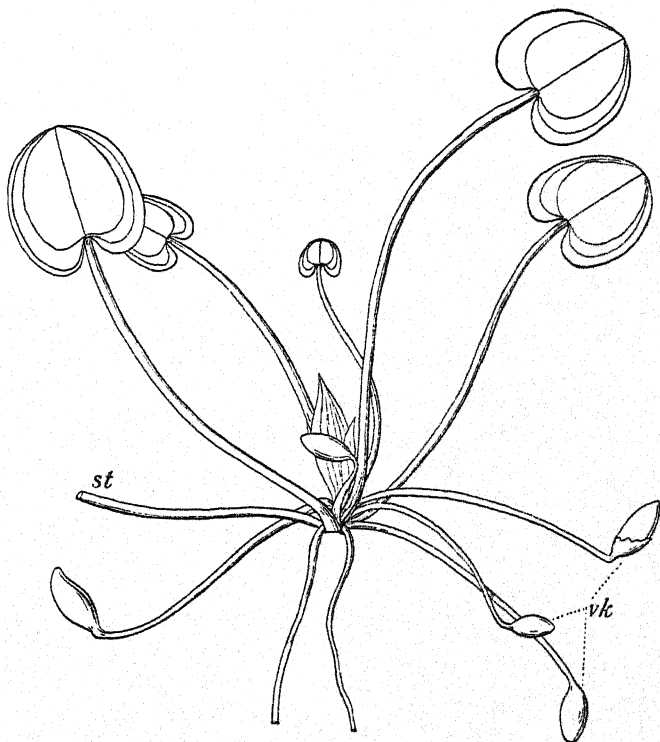
FIG. 76. *Hydrocharis morsus ranae*; a free-swimming plant in the autumn stage. From the leaf axils arise short stolons each with a winter bud, *vk*, at the apex. When the winter buds have attained their full size and are filled with food material they fall off and sink to the bottom; the mother plant then dies. Later on, in the spring, the leaves of the winter bud begin to separate, and air-bubbles are developed which are held between the leaves, making the specific gravity of the buds less than that of the water, so that the buds rise up to the surface, where the leaves unfold. (*c.* †)

contradicted by what happens in nature. I have several times seen, for example in *Typha latifolia*, that the stolons growing freely out in the water but entirely overshadowed by the densely packed aerial shoots, grew horizontally as long as they were in the shade, but obliquely downwards as soon as they reached the edge of the community, where they were exposed to the light. Nevertheless, even if light is present so that the rhizome grows obliquely downwards, it is undecided whether the

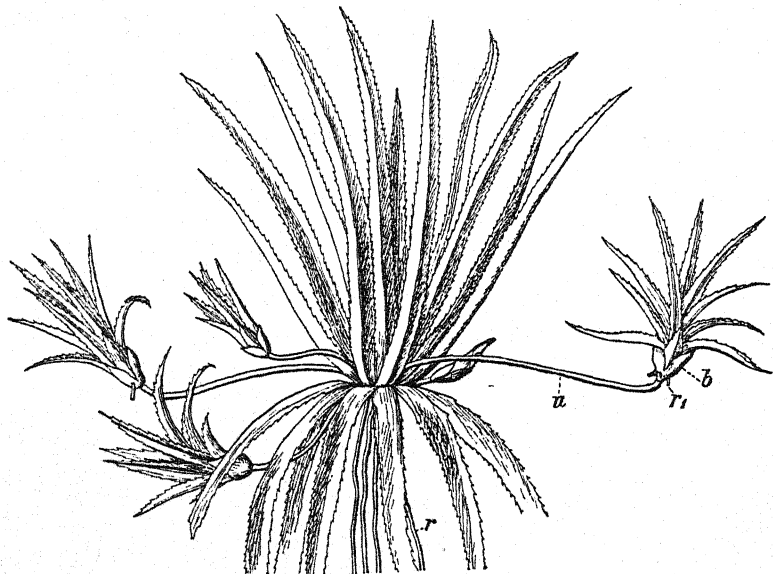FIG. 77. *Stratiotes aloides*, free-swimming water plant; in the leaf axils arise stolons of varying length each with a rosette (a young plant) at the apex. In the autumn the fully developed leaves die, and the shoot-apices with the young leaves sink down to the bottom of the water, where they survive the winter.

changed direction of growth is due to negative heliotropism or to positive geotropism.

29. **Hydrophytes.** These plants survive the unfavourable season by means of buds which lie at the bottom of the water; the vegetative shoots are sunk in the water, and only the flowers or the inflorescence rise above the surface for pollination. The leaves are either completely submerged or the leaf laminae rest on the surface of the water (floating-leaves); the submerged leaves are either very narrow, or, if they are broad, divided into linear segments (gill-leaves). The floating leaves are undivided or orbicular, ovate or ovate oblong; the base is usually cordate.

Some Hydrophytes have rhizomes that grow at the bottom of the water, and the winter buds are found on these rhizomes, as in *Nuphar*, *Nymphaea*, *Zostera*, *Aponogeton*, *Limmanthemum*, *Helodea*, species of *Potamogeton* (Figs. 74 and 75). Others on the contrary do not have

perennating rhizomes; but at the beginning of the unfavourable season the plant dies entirely except for certain winter buds which become detached from the plant, sink to the bottom of the water, and there survive the unfavourable season. Several of these plants are rooted, e.g. *Potamogeton zosterifolius*, *P. acutifolius*, *P. mucronatus*, *P. obtusifolius*, *P. pusillus*, and others. Others are free swimming with roots, e.g. *Hydrocharis* (Fig. 76) and *Stratiotes aloides* (Fig. 77), or without roots (species of *Utricularia*). Those Hydrophytes that survive the winter season by means of buds at the bottom of the water show the widest adaptation to periods unfavourable for growth. Between this type and the evergreen Megaphanerophyte with naked buds seen in the tropical rain forest lie the whole series of degrees of adaptation represented by the series of types that have been described.

V. THEROPHYTES

30. **Therophytes** are plants of the favourable season, or 'summer-plants'. In this category I place plants which survive the unfavourable season in the form of seed; but they complete their entire life-history from seed to seed during the favourable season, and many of them can run through the whole cycle in as short a period as a few weeks. Since seeds, because of their firm close testa, are among the parts of plants which are best protected against drought, these plants are able to live in regions with a very hot and dry climate, and only a short favourable season; steppes and deserts are comparatively rich in Therophytes. This life-form occurs also indeed in many other situations, but especially on cultivated land where there is much open ground. Many of the annual plants occurring on cultivated ground have presumably arisen as a result of cultivation by unconscious selection of variations whose life-history corresponds with that of the annual crop, and whose seeds therefore ripen and are harvested together with the crop. Besides the annual summer plants which complete their life-history during a single summer I reckon as belonging to this type at least some of the annual plants which survive the winter, and which in our climate germinate in the late summer or autumn, and pass the winter in the form of rosettes from which flowering shoots are produced during the next spring. At first sight one might suppose that these plants, like biennials, should be reckoned among the Hemicryptophytes. Those annuals which survive the winter and which can also be biennial I count as Hemicryptophytes, e.g. *Lepidium ruderale*, *L. campestre*, *Torilis anthriscus*, *Chaerophyllum temulum*, *Jasione montana*, *Carlina vulgaris*; and also those which besides surviving a single winter may grow as perennials, e.g. *Myosotis arvensis* and *M. silvatica*.

But those species which either invariably behave as annual plants lasting through the winter, or may also be ordinary annuals, I reckon

among the Therophytes: examples of the first group are *Schedonorus tectorum, Draba muralis, Alyssum calycinum, Anthriscus vulgaris,* and many others. Examples of the second group are *Bromus arvensis, B. commutatus, B. mollis, B. secalinus, Cerastium semidecandrum, C. glomeratum, Arenaria serpyllifolia, Draba verna, Thlaspi arvense, Teesdalea nudicaulis, Arabis thaliana, Scandix pecten Veneris, Galium aparine, Veronica hederifolia, Centaurea cyanus, Anthemis arvensis, Crepis tectorum, C. virens,* &c., &c.

The fact that these plants survive our winter but not our midsummer leads us to suppose that it is the dry summer and not the cold winter which is the unfavourable period for them, and that they come from regions with a summer hotter and drier than ours. Nearly all our species are found in the Orient.

Most of the plants which grow as annuals with us are not native in this country. It is only because they grow on cultivated soil, where the interference of man protects them from competition with perennial plants, that they are able to exist. If the ground were left to itself most of the annuals would succumb in the battle with other life-forms.

THE USE OF LIFE-FORMS IN PLANT GEOGRAPHY TO CHARACTERIZE EQUICONDITIONAL REGIONS

Geography is the study of the Earth, especially in relation to its suitability for cultivation and its importance as a habitation of man. In this science the plant world plays the most important role, partly directly, by yielding cereals, &c., and partly indirectly by fulfilling the demands of animals.

The different character of vegetation in the various regions of the world results from the difference in the essential qualities of the unfavourable season. If, for example, the climate of Denmark at all seasons resembled our best summer weather, then a number of tropical and subtropical plants, including cultivated plants, would certainly thrive here. They do indeed grow remarkably well here in the summer. This is of course not true of all parts of the world; towards the poles even the most favourable period is too cold for plants belonging to hot regions. But at any rate it is true that if the climate throughout the year in every region resembled the climate of the most favourable season of the region, then a great number of plants, including cultivated plants, would have a much wider distribution than they have at present. It is especially the unfavourable season which limits their distribution.

Our task is to describe a region in terms of the plant world, but we are not concerned so much with purely botanico-biological affairs. We must also consider factors which make plant cultivation possible, and stock raising, which follows as a sequel, and also the suitability of the region as a habitation of man, which is dependent both on the plants and

on the animals. This task is best accomplished by considering how plants behave during the unfavourable season, and to what extent this season hinders the existence of the life-forms to which different cultivated plants belong. It is therefore the metamorphosis of the plant body enabling it to survive unfavourable seasons which I have taken as a foundation for the life-forms I have described; they are biological types corresponding to different climates.

It is of course not true that plants in a definite climate all belong to one single life-form; but the main types of climates are characterized by the fact that one or few life-forms are, relatively or absolutely, dominant. This can be expressed numerically; the plant-climate can be characterized by a statistical survey of the life-forms. How this can be done I will show by some examples.

Here, however, we encounter a difficulty. The flora of no country has been investigated so thoroughly that the information available in books is sufficient to enable any one to decide to which life-form each individual species belongs. In some floras this can be decided for the majority of species; but for a statistical investigation all of the species, as far as possible, must be included. By investigations of the Danish flora carried out for many years I have tried to procure all the information necessary for determining the life-form of all our species, so that it is now possible to decide with some certainty the percentage of Danish species belonging to each life-form described in this book. As we shall see later, for the sake of comparative investigation it is better to reduce the number of the life-forms used.

But first we must consider how to determine the number of species. For the time being I include only flowering plants. I omit vascular cryptogams because they are not often included in lists of the higher plants of a country or a district. If they were included here a comparison between the statistics of life-forms in Denmark and other regions would encounter the difficulty that the comparison did not rest upon a uniform foundation, as of course it should.

Next we must decide which species should be included among the flowering plants. Besides the aboriginal plants, we have here, as in most other places, many species which mankind in the course of time has either voluntarily or involuntarily introduced. It is often difficult to decide whether a species has reached the country with or without the aid of man; but this is not the most important thing. It is a matter of no consequence whether a species has been introduced by the wind, by animals, or by man. Man is as much a part of nature as animals are. What seems to be decisive is that the species in question can maintain a place for themselves in our flora without the assistance of cultivation. The species which can do this I regard as belonging to the flora; and it will be apparent that these species, both here and in other regions, belong

to the locally dominant life-form or life-forms, so that it does not influence the statistical result whether they are included or omitted. I exclude on the other hand all species which are dependent upon man, such as numbers of weeds in fields and gardens, especially Therophytes, which in our climate can only persist on constantly cultivated ground, where they have not to compete with the dominant life-form of this region, the Hemicryptophytes.

The flora of Denmark thus limited contains 1,084 species. We shall see later what proportion belongs to each life-form. Here it may be remarked that only 75 species (7 per cent.) are Phanerophytes, while 538 species (about 50 per cent.) are Hemicryptophytes. The numerical superiority of the Hemicryptophytes makes it probable that the Hemicryptophyte is the characteristic life-form of the plant-climate of Denmark. But at this stage we cannot be certain of this fact, for it is possible that Hemicryptophytes preponderate in every flora. We are not certain of our facts till we make a comparison between the floras of different climates.

Even if no other country or region has been investigated sufficiently to enable us to give a comparative account of the life-forms as we can for Denmark, yet there are a great many regions of which sufficient is known of the flora to enable us to say that the species are distributed among life-forms in a manner widely different from the Danish species. We know for example that in all tropical countries where the dry season is not too severe it is the trees (Phanerophytes) which dominate the other life-forms. But of the actual relative percentage of life-forms among the species we can say nothing until all the life-forms of all the species are known. The floristic handbooks of to-day resemble in this respect those written a hundred years ago. Herbaceous Chamaephytes, Hemicryptophytes, and even a number of Geophytes are included under the designation of 'Perennial Herbs'. For Phanerophytes, trees and bushes, often the height is not mentioned; and as a rule there is no information about the covering of the buds or whether the plants are deciduous or evergreen. One can indeed often find out from books whether the woods of a district are evergreen or deciduous; but as it often happens that in a region with evergreen woods deciduous trees also occur, and since in regions with deciduous woods (e.g. Denmark) there are evergreen species, it is not possible to use statistics based on the fact that the woods are evergreen or deciduous. It is obvious then that the floristic handbooks stand in need of enrichment with biological material, and that it is exceedingly desirable that those studying the flora of individual regions should strive to include in their books information about the life-forms of each species, or at any rate information sufficient to enable others to determine the life-forms. It is often considered superfluous to give life-forms of every species; but this must be done.

In the latest edition of my *Dansk Ekskursionsflora* I have added to the descriptions the main type of life-form to which each species belongs; but the information given is not quite complete; e.g. the Beech is marked as a Phanerophyte, but that it is deciduous is not mentioned. It is however mentioned when trees and shrubs are evergreen; if they are deciduous it is not so stated. I have allowed it to be taken for granted that a Phanerophyte is deciduous unless it is stated as being evergreen, because the majority of our Phanerophytes are deciduous. But this method is wrong and must eventually be altered. We must bear in mind that in Japan or some other distant country botanists might be making use of a list of plants of Denmark for comparative study. For these botanists it is very far from self-evident that a certain Danish tree is deciduous, and that all of them are not deciduous. We are placed in the same position in dealing with the floras of distant countries. I have attempted in vain to determine from books the relative numbers of ever-green and deciduous plants in different floras, e.g. New Zealand. We know indeed that most of the Phanerophytes of New Zealand are evergreen, and we also know that some of them are deciduous; but in the floras of New Zealand it is not stated which are evergreen and which are deciduous.

Since it was important for me to obtain for comparative purposes the numerical relationship of the life-forms in a climate widely different from our own, and since this information was not available in books, I was obliged to undertake a journey myself. During 1905 and 1906 I visited the West Indies with the object of finding out the life-form of all the species, as far as possible, in a sharply bounded and accessible territory with a climate very different from that of Denmark.

For comparison with Denmark I have chosen the Isles of St. Thomas and St. Jan. Besides the indigenous species I include also, as for Denmark, those plants that have been introduced and which appear to be naturalized. This brings the number of species to 904, and I shall now show how they are divided among the various life-forms.

As I said before it is best to diminish the number of life-forms used. There are two reasons for this. Firstly, it is not necessary for the por-trayal of plant climatic territories to use as many life-forms as I have defined in this book. Secondly, for a long time to come the data available for determining some of the life-forms will not be procurable for all species, at any rate for the regions less frequented by botanists. This is true for example of bud-scales. Thus among the Phanerophytes those with covered buds and those with naked buds are not here distinguished; we must content ourselves with stating whether or not bud-scales appear to be dominant. Unfortunately we cannot for the time being distin-guish between evergreen and deciduous plants, because our information about individual species is insufficient to enable us to do so. But so many accounts given in general terms are available that this want can be

supplied by observing which condition is the commoner. Further, Megaphanerophytes and Mesophanerophytes are treated as one group: Herbaceous Phanerophytes are united to Nanophanerophytes: Hemi-cryptophytes are all treated as one life-form, as are also Chamaephytes; and lastly the seven groups of Geophytes are reduced to two, viz. Geophytes proper as one group and Hydrophytes and Helophytes as the other. Thus the thirty life-forms are reduced to ten.

It is needless to say that investigators should do all they can to decide to which of the thirty life-forms the individual species belong. The number of life-forms can always be reduced if this is necessary for purposes of comparison.

The table below shows the flowering plants of Denmark in one column and those of St. Thomas and St. Jan in the other column, divided into ten main life-forms.

Further explanation is unnecessary; the numbers express at once the essential relationship between the climate and vegetation, i.e. the plant climate. That of Denmark is a Hemicryptophyte climate (half of the plants belonging to this life-form). In the islands of St. Thomas and St. Jan the majority of the species (53 per cent.) are Microphanerophytes and Nanophanerophytes. In Denmark only 6 per cent. of the species belong to these groups. For the West Indies it can further be added that almost all Phanerophytes are evergreen, and that a number, especially the tall ones, have bud-scales.

	Denmark. 1,084 species. per cent.	St. Thomas and St. Jan. 904 species. per cent.
1. Megaphanerophytes and Mesophanerophytes . . .	1	5
2. Microphanerophytes	3	23
3. Nanophanerophytes	3	30
4. Epiphytes	0	1
5. Stem succulents	0	2
6. Chamaephytes ·	3	12
7. Hemicryptophytes	50	9
8. Geophytes	11	3
9. Hydrophytes and Helophytes	11	1
10. Therophytes	18	14

(Now if we knew the life-forms of the plants of all regions as well as we know those of Denmark and the Danish West Indies, we could then portray the climate of each individual region by means of a numerical conspectus, showing how the plants of each region were divided among the different life-forms. But for limiting the boundaries of the different plant climates there is another want to be supplied; there is no guiding principle to show where the boundaries are to be drawn.) Let me illustrate this by an example.

The plant climate of North and Central Europe is characterized by

a preponderance of Hemicryptophytes. If we go towards the south the Hemicryptophytes decrease, and when we reach the Mediterranean region it is other life-forms, e.g. Chamaephytes and Nanophanerophytes, which preponderate. But there is no guiding principle to tell us how far the number of Hemicryptophytes must fall before we can say that this life-form no longer characterizes the climate. We lack a common measure with which to compare all regions, and this common measure is the percentage of life-forms among all the species of plants in the world. But while such a common measure ought to be the starting-point for our demarcation of plant-climates, as a matter of fact, because of our present ignorance of the life-forms of species, it comes to be the final result of our investigations, if not their ultimate object. To overcome this difficulty I have conceived and also begun to apply the following method. In order to discover the percentage of the different species composing the various seeds in a mixture we must be content with finding this out from samples. In the same way we must determine the percentage of individual life-forms in the flora of the world by determining their relative frequency in a considerable number of species selected at random. Here we encounter at least two difficulties. Firstly, species whose life-form is to be determined must be chosen in such a way that they can be looked upon as a true picture of all the species in the world. But this may be done approximately by taking a certain number, say a thousand species, from an alphabetical list of all known species.

The second difficulty is to discover the life-forms of these thousand species; because of the method of choosing the species one is likely always to hit upon plants about which little is known. But by contenting oneself with the ten groups of life-forms used above this difficulty can be overcome. Investigations of this kind give us a common measure by which the individual floras can be compared, and by means of which the bio-geographical character of the flora can be determined, because the plant-climate of the individual regions will be characterized by the life-form or the life-forms whose percentage rises above the percentage in the common measure. And the higher the rise of the number above that of the common measure the more strongly the life-forms in question characterize the plant-climate of the region.

It thus becomes possible to draw with certainty bio-geographical lines limiting regions which possess, taken as a whole, uniform requirements for cultivation. Such boundaries must be drawn where the percentage of given life-forms rises above their percentage in the common measure. If, for example, we are to draw a boundary line between the Hemicryptophyte climate of Central Europe and the climate of the Mediterranean region, which is characterized by Chamaephytes, Nanophanerophytes, &c., we must go southward, making biological statistics by investigations of the local floras, till at length we come to regions where the percentage

of Hemicryptophytes falls below the number in the common measure, and where, therefore, it can no longer be said that Hemicryptophytes characterize the climate. Of necessity the percentage of one or more other life-forms will have risen above that of the common measure, and it will be these life-forms that now characterize the climate. Such a change always indicates a bio-geographical boundary. Gradually, as the biological study of the vegetation of individual regions advances, we shall be able in this way to divide the earth's surface into phyto-climatic regions and provinces in which are found uniform conditions for plant life and correspondingly uniform conditions for cultivation.

Such an investigation in addition to its bio-geographical interest has also a very important botanical aspect. Gradually, as the bio-geographical investigation of the plant-climates of the world proceeds by determination of the life-forms of the individual species, we procure a mass of biological and morphological facts, suitable for use in monographs dealing with the biology and morphology of the vegetative organs within the individual families. In this way it will be possible to give a comparative picture of life-forms in the individual families, showing how the behaviour of the vegetative organs and the life-forms determined by their behaviour alter in harmony with the regions of geographical distribution of the individual families. It is hoped to obtain by these means an historical explanation of the morphology of the vegetative organs, an explanation of the various morphological transformations that are encountered in the individual families, in correspondence with their distribution in different climates in the past and at the present time.

By studying adaptations to climate we shall find out whether species have arisen by mutation or whether variation brought about by environment have in the course of time become hereditary.

This chapter is no more than a small contribution to our knowledge of a small territory within Nature's far-flung domain. And even if, as it seems to me, from the point we have reached, paths can be seen that lead forward, yet the distant goals of which glimpses are caught lie so far away that one investigator can never reach them.

Many paths lead to those distant goals; and when one goal is reached, indeed often long before, fresh ones loom forth, firing the traveller with enthusiasm to reach them. As it has been the destiny of every investigator so shall it continue to be; his mind is not filled with apprehension, but rather braced for fresh efforts and the strings of his heart are tightened and tuned, in harmony, let us hope, with the unknowable. Only a short way does one investigator penetrate into Nature's land of mystery; but his efforts are not in vain, for the marvels of his observations, happiness in his work, and joy of recognition are his wages and his daily bread.